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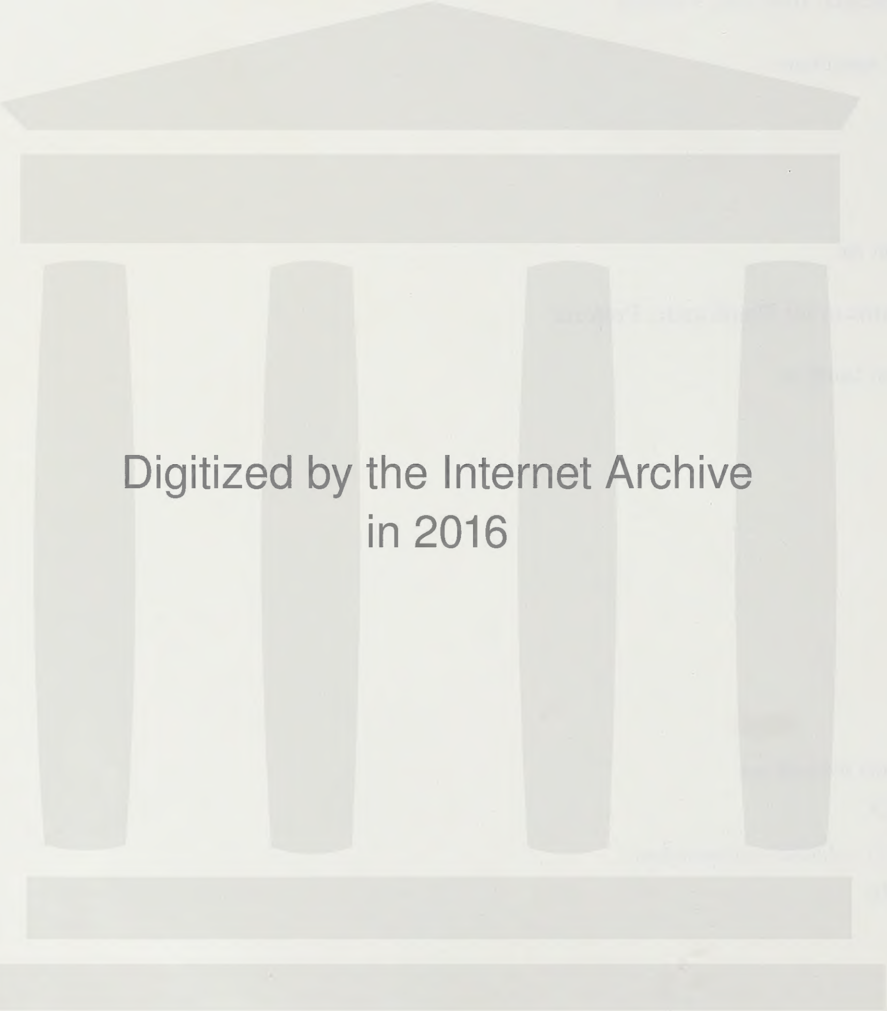

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The collecting activities of Anton Rehmann (1840–1917) in South Africa

L. E. CODD* and MARY GUNN*

ABSTRACT

Anton Rehmann undertook two collecting expeditions in South Africa, in 1875–77 and 1879–80, during which he collected over 9 000 numbers. The latter journey took him as far north as the Houtbosch in Transvaal, where he was the first to make an extensive collection. A brief account is given of his life and his itineraries in South Africa with details, as far as can be ascertained, of his collecting localities.

INTRODUCTION

Since completing the note on Anton Rehmann for Botanical Exploration in southern Africa (Gunn & Codd, 1981), additional information has been found. At the cost of some duplication, this information is now presented.

None of Rehmann's diaries or plant registers has been traced so one must rely largely on plant specimens for information on his localities and the routes he followed. The main sources of information on his South African flowering plants are the two papers by Szyszylowicz (1887, 1888) and, to a lesser extent, citations of his specimens in revisions appearing in Flora Capensis from Vol. 4 onwards, and in other publications. His mosses were dealt with by Dixon & Gepp (1923) from which it is apparent that the numbering system he used for the mosses differs from his method of numbering the phanerogams and ferns.

LIFE HISTORY

Anton Rehmann was born on 13 May 1840 in Cracow (Kraków or Krakau) which is now in southern Poland, but was then in the Austro-Hungarian Empire in the province of Galicia, a region lying north of the Carpathian Mountains (Fig. 1). He died on 13 January 1917 in Lvov (or Lwów), previously known as Lemberg, situated in the eastern part of Galicia which, after World War II, was included in the Ukraine. No information on his family background has been discovered, but it is generally agreed that Rehmann is not a name of Polish origin, and that he was probably of German ancestry. The genus *Rehmannia* Libosch. is named after Joseph Rehmann (?–1831), a successful medical practitioner, who was born in Freiburg-im-Breisgau (Pritzel, 1871) and later emigrated to Russia, becoming one of the leading physicians at the court of St Petersburg. His slender link with botany rests on a small book which he wrote on Tibetan Pharmaceutics. Another Rehmann to appear briefly in botanical literature was A. (or E.) Rehmann who, in collaboration with F. Brunner, wrote: 'Gaea und Flora der Quellenbezirke der Dona und Wutach', given out by the Naturforschende Gesellschaft, Freiburg-im-Breisgau, 1851 (Catalogue of the Library of the British Museum, Nat. Hist.).

Our Anton Rehmann wrote in German and Polish with equal fluency. When he published articles in Polish he spelt his name with one 'n', but when writing in German he spelt it Rehmann. In an obituary written in Polish by Rouppert (1917), his name is rendered as Antoni Rehman.

FIG. 1.—Anton Rehmann (1840–1917), by courtesy of the Hunt Institute for Botanical Documentation.

Rehmann showed an early interest in botany and must have been an enthusiastic collector because he started assembling a personal herbarium while still at high-school. In 1860 he attended the Jagiellonian University, Cracow, graduating in 1863. The following year, as assistant to Prof. Czerwiakowski, he obtained the Ph.D. degree. His first publication in 1862 dealt with the ferns and bryophytes of western Galicia, the region around Cracow, and in 1864 he expanded this into a more extensive geobotanical study, delineating the main vegetation zones of western Galicia and listing the bryophytes characteristic of each zone. In 1866–67 he studied in Munich, receiving his 'docent' degree, and returned to Cracow in 1868. Here he continued with his floristic studies of Galicia and the adjoining Bukovina, with particular reference to the flora of the Carpathian Mountains. In 1873 he published his

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first paper on *Hieracium,* a genus which was to occupy much of his attention in later years.

At the age of 35, and having done some travelling in central Europe, he embarked on the first of two lengthy expeditions in South Africa. After his first visit in 1875–77 he published a paper (Rehmann, 1879) entitled 'Geo-botaniczne stosunki poludniowéj Afryki' (Phytogeographical conditions in South Africa), in which he included a map showing broad phytogeographical regions and indicating the route which he followed (Fig. 2).

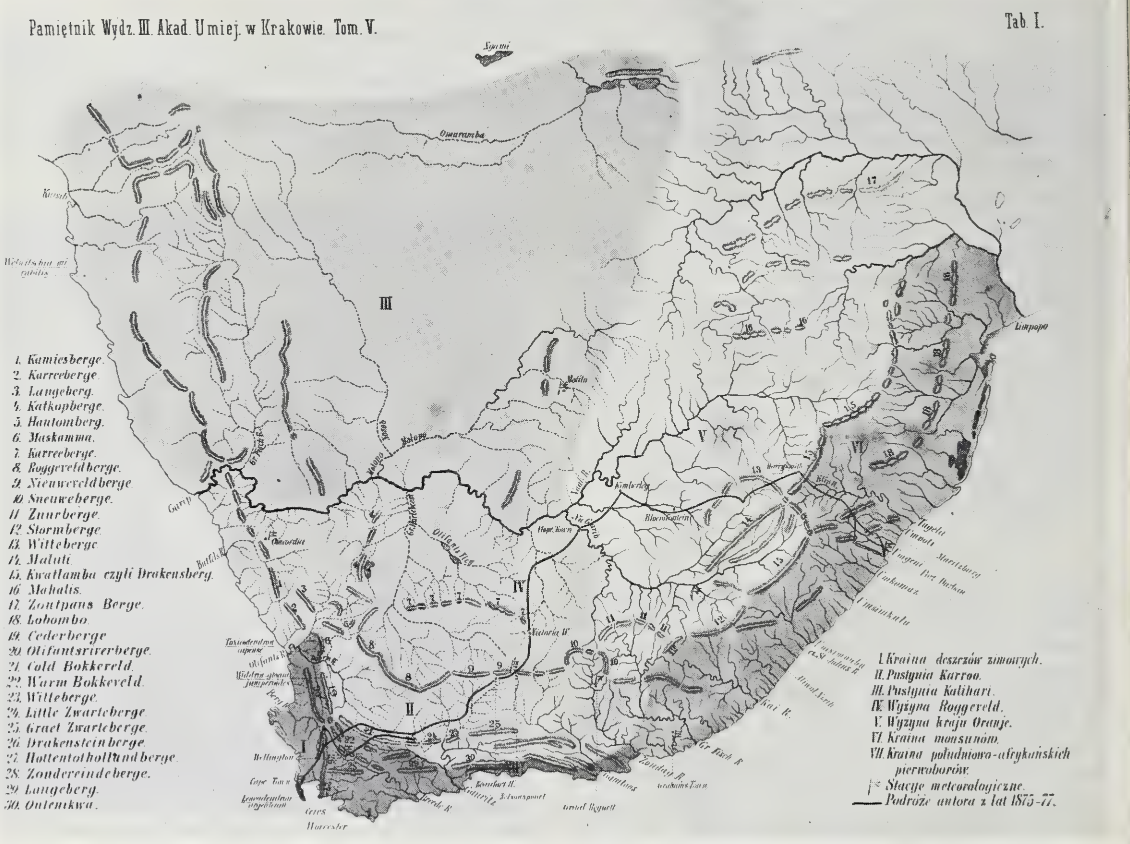


FIG. 2.—Route followed by Rehmann during his first visit 1875–77 (Rehmann, 1879).

On his second visit during 1879–80 he concentrated on the Transvaal, travelling as far north as the Houtbosch (Woodbush). Although he was not the first person to collect in this area, he was certainly the first to make a substantial collection. William Nelson preceded him in February–March 1878 and Canon William Greenstock gathered a few specimens when he visited the area in August 1875. On his return to Cracow he wrote 'Das Transvaal-Gebiet des südlichen Afrika in physikalisch-geographischer Beziehung' (Rehmann, 1883), including a map on which his routes are indicated. Unfortunately, our copy of the map is not clear enough for reproduction. It is based on Jeppe's map of 1879, portion of which is reproduced in Fig. 9, but lacks the minor localities. The article is disappointing in its lack of any botanical information. Not all his collecting localities are shown on the two maps which he published and the subject of his itineraries and collecting sites is discussed in some detail later.

In 1882 he was appointed Professor of Geography at Lemberg University and, although he paid some attention to the genus *Hieracium,* most of his time was devoted to geographical and ethnographical studies. His best known work was entitled 'Ziemie dawnej Polski i sasiednich krajów slowiańskich' (The land of ancient Poland and the neighbouring Slav regions), Lwów, I (1895), II (1904).

REHMANN'S PHANEROGAMS

Shortly after his appointment to Lemberg, Rehmann made his South African phanerogams available to Ritter Ignacy (Ignaz) von Szyszylowicz (1857–1910), who also graduated from the Jagiellonian University, Cracow and, after further study in Germany, worked in the Natural History Museum, Vienna, from 1885 to about 1891. He later became head of the Experimental Station for Agricultural Botany at Lemberg (Lwów) and extraordinary Professor of Botany at the University. Szyszylowicz (Figs 3 & 4) started writing up Rehmann's plants for publication but, after two parts had appeared (1887, 1888), there seems to have been some disagreement between the two because all the plants were returned to Rehmann, who sold them to Schinz of Zurich (according to a letter dated May 1889 from

N. E. Brown to MacOwan, part of which is reproduced in Fig. 5).

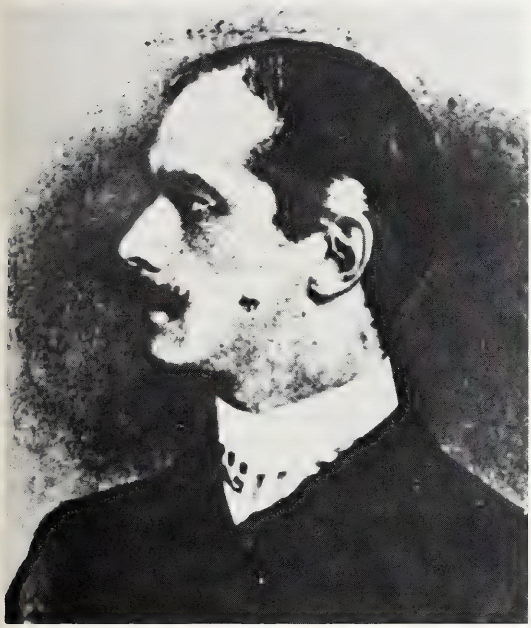
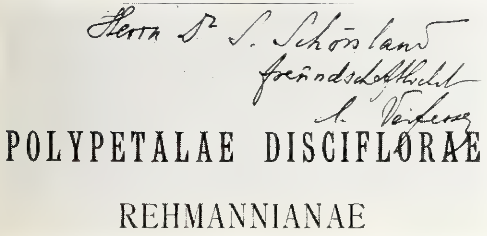


FIG. 3.—Ignacy von Szyszylowicz (1857–1910), by courtesy of the Hunt Institute for Botanical Documentation.



Herrn Dr S. Schönland
freundschaftlichst
I. Szyszylowicz

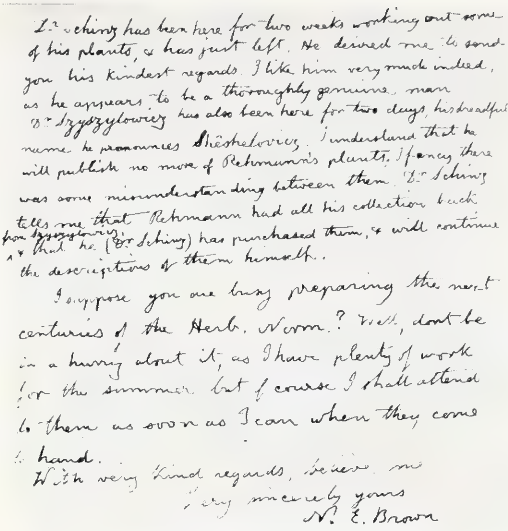
POLYPETALAE DISCIFLORAE

REHMANNIANAE

FIG. 4.—An example of Szyszylowicz's handwriting.

From the two publications by Szyszylowicz it is possible to obtain some idea of the magnitude of Rehmann's collection and of the routes which he followed. Szyszylowicz listed about 1 073 Rehmann specimens, which were included in 421 species. The highest collecting number noted was 9067, which would indicate that Rehmann probably collected well over 3 000 species. The lowest number cited was No. 141, *Empleurum serrulatum* Ait., from 'Outeniqua Mts: Montagu Pass'. The numbers and associated localities are listed in detail at the end of the present paper, but the sequence derived from Szyszylowicz, according to provinces, may be summarized as follows: Cape Province 141–3 233, O.F.S. 3 351–4 006, Transvaal 4 083–6 837, Natal 6 883–9 067.

His specimens, with a few exceptions mentioned below, bear a standard printed label (Fig. 6): 'Dr. A. REHMANN: Exsiccata Africae austr. ex ann. 1875–1880'. On the label there is also a number (hand-written), the province (printed) and locality (rubber stamp). The absence of a specific collecting date on each label is an unfortunate omission. Apart from not providing an indication of the time of year at which a plant was collected, the only clue to the sequence of Rehmann's collecting activities is the number on the label, a subject which is discussed in some detail later.

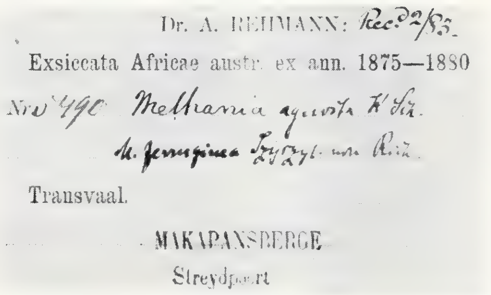


Dr Schinz has been here for two weeks working out some of his plants, & has just left. He desired me to send you his kindest regards. I like him very much indeed, as he appears to be a thoroughly genuine man. Dr Szyszylowicz has also been here for two days, his dreadful name he pronounces Shëshelovicz. I understand that he will publish no more of Rehmann's plants. I fancy there was some misunderstanding between them. Dr Schinz tells me that Rehmann had all his collection back from Szyszylowicz, & that he (Dr Schinz) has purchased them, & will continue the descriptions of them himself.

I suppose you are busy preparing the next centuries of the Herb. Norm.? Well, dont be in a hurry about it, as I have plenty of work for the summer, but of course I shall attend to them as soon as I can when they come to hand.

With very kind regards, believe me
Very sincerely yours
N. E. Brown

FIG. 5.—Part of a letter dated May 1889 from N. E. Brown to MacOwan.



Dr. A. REHMANN: Recd 2/83

Exsiccata Africae austr. ex ann. 1875—1880

Nro 490 Melhania agrosta K Sch.

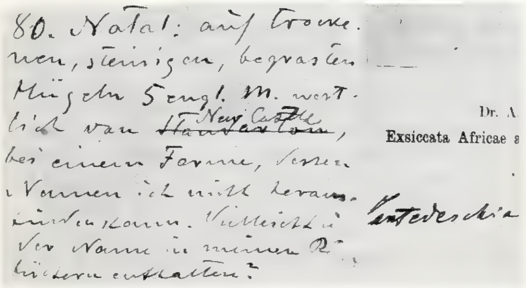
M. ferruginea Szyszyl. non Rich.

Transvaal.

MAKAPANSBERGE

Streydpoort

FIG. 6.—Standard label on Rehmann's phanerogam and fern specimens.



80. Natal: auf trockenen, steinigen, begrasten Hügeln 5 engl. M. westlich van New Castle ~~[illegible]~~, bei einem Farmer, dessen Namen ich nicht herausfinden konnte. Vielleicht ist der Name in meinen Büchern enthalten?

Dr. A

Exsiccata Africae

Zantedeschia

FIG. 7.—Temporary label on a Rehmann specimen, the type number of *Zantedeschia rehmannii*, in Z.

When Rehmann returned to Cracow in 1880, Engler was working on revisions of the Araceae, Anacardiaceae and Burseraceae, the last two for the series of De Candolle's Monographiae phanerogamarum. Probably at the request of Engler, who was then at Breslau University, Rehmann quickly packed off material of these three families to him. The *Zantedeschia* specimens, which were examined some years ago (see Letty in Bothalia 11: 11, 18, 25; 1973), bear labels which differ from the standard kind with numbers in a different series. The fact that two specimens (83 and 7096), obviously duplicates of one gathering, bore different numbers and localities indicates they were sent off in haste; probably the sheet labelled 83 was sent to Engler and the sheet labelled 7096 was kept back and received its label later. Engler apparently retained some duplicates (e.g. No. 82), but the majority were returned to Rehmann. The specimens of *Zantedeschia* in Zurich, which Rehmann sent to Engler, are listed below. The labels were written by Rehmann, but the determinations are usually in Engler's handwriting (Fig. 7).

72. *Z. macrocarpa* Engl.?: Natal, Laingsnek.
80. *Z. rehmannii* Engl.: Natal, New Castle.
82. *Z. macrocarpa* Engl.: Transvaal, Trigardsfontein.
83. *Z. macrocarpa* Engl. (*sic*): Transvaal, Trigardsfontein.
    Although labelled Trigardsfontein, this locality appears to be wrong. Another sheet in Z, obviously a duplicate of the sheet No. 83, has a standard label with the number 7096 and the rubber-stamped locality 'Drakensberge, Biggarsberge' on it. The specimens are of leaves only, but they are recognizable as *Z. albomaculata* subsp. *valida* Letty, which is known only from the Biggarsberg area.
92. *Z. aethiopica* (L.) Spreng.: Transvaal, Houtbosch.
93, 94. *Z. albomaculata* forma *latifolia* Engl.: Transvaal, Houtbosch.

Not only do the above numbers differ from the standard series, but they run in the reverse order, from Natal to the Transvaal, not *vice versa*. The number 7096 fits in with the numbering of other plants in the series finally adopted (see later). It is apparent that Rehmann gave his specimens their final numbers after returning from his second visit and not in the field.

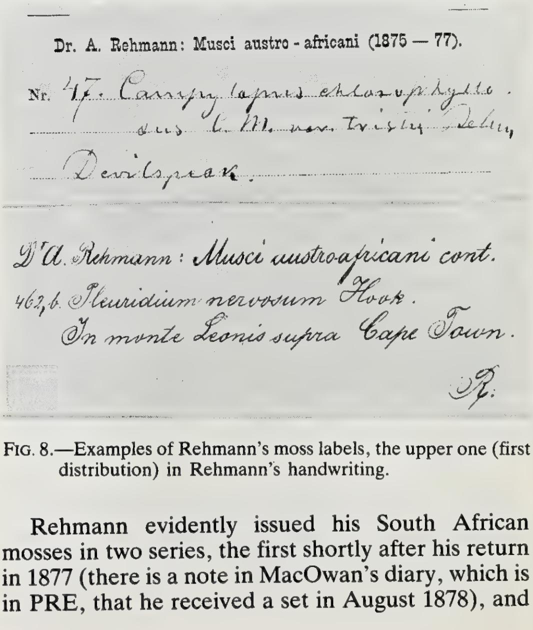
At the end of his second expedition, Rehmann called on Medley Wood and obtained some duplicates from him, including mosses, a group in which Rehmann was particularly interested. He then stopped off in Cape Town for a week or two during his return voyage and there is a note in Harry Bolus's diary that Rehmann visited him on 16 and 23 May 1880. On the latter occasion Bolus handed over McLea's entire moss collection to Rehmann on the understanding that Rehmann would keep a set and return the remainder, named and numbered, together with a set of his own Cape mosses. Rehmann also undertook to let Bolus have a set of his Transvaal flowering plants in return for a parcel of Bolus's duplicates.

While in Vienna, Szyszylowicz had access to rich holdings of South African Herbarium material. So, in addition to citing specimens of other collectors, such as Wood, Bolus, MacOwan and Tyson, which could have been acquired by Rehmann, he records having seen specimens collected by Ecklon and Zeyher, Drège, Scholl, Krauss, Gueinzius, Cooper, Baur, Weale and Spilhaus.

REHMANN'S MOSSES

Information on Rehmann's mosses is derived mainly from Dixon & Gepp (1923) whose work was based on the material at K and BM, supplemented by a manuscript list drawn up by T. R. Sim from the sets of Rehmann mosses which he had seen in South African herbaria. These sets were acquired by Bolus, MacOwan and Medley Wood, and are now in BOL, GRA and NH, respectively. None of the sets is complete and there is not a great deal of duplication, suggesting that one fairly full set was divided between the three herbaria. The Rehmann material in Sim's personal herbarium, now in PRE, consists of fragments derived from the specimens in BOL and GRA. Strangely enough, there is no direct evidence that Sim consulted the NH material.

The Rehmann specimens were first classified into genera, species and varieties before numbering, and the numbers run from 1 to 680. There were, however, more gatherings than this because, if a species or variety was collected at more than one locality, the additional gatherings were labelled with b, c etc., so that 665, 665b and 665c represent three different gatherings of the same species. Sim's MS list accounted for about 500 of the 680 numbers and Dixon & Gepp filled in many of the gaps from K and BM material, leaving about 50 numbers unaccounted for.


Dr. A. Rehmann: Musci austro-africani (1875 — 77).

Nr. 47. Campylopus chlorophyllus C. M. var. tristis Rehm, Devilspeak.

Dr A. Rehmann: Musci austroafricani cont.

462,b. Pleuridium nervosum Hook.

In monte Leonis supra Cape Town.

R.

FIG. 8.—Examples of Rehmann's moss labels, the upper one (first distribution) in Rehmann's handwriting.

Rehmann evidently issued his South African mosses in two series, the first shortly after his return in 1877 (there is a note in MacOwan's diary, which is in PRE, that he received a set in August 1878), and the second series in or before 1886. The first series consisted of Nos 1–423 (or 424, which is a blank) and the second of Nos 425 (or 424)–680. Whereas all the specimens in the first series were collected by Rehmann, considerably less than half the specimens in the second series were collected by him. A rough count revealed that about 159 of the latter were collected by McLea, 20 by Medley Wood, 3 by MacOwan, 3 by Buchanan and 1 by Drège. Rehmann attached many provisional new names to items he considered were new species or varieties, but never published any of them.

According to Urban (1916, p.124), Rehmann's extensive moss herbarium, which included material from all over the world gathered by various collectors, was acquired by Berlin-Dahlem in November 1892. It was reputed to contain 2 800 South African specimens (about 500 species) among which were many novelties. Many of the latter were described by C. Müller in Hedwigia 38: 52–155 (1899). Dixon & Gepp (1923) drew attention to discrepancies in Müller's method of numbering Rehmann specimens: he sometimes cited a "Musci austro-africani" number which corresponds with Dixon & Gepp's list, sometimes Rehmann's collecting number as 'Rehm. coll.' and sometimes no number at all. Unfortunately this valuable material was almost entirely destroyed during World War II so it is not possible to determine if the erratic numbering was due to Rehmann or to Müller — probably the former. It is a great pity that Dixon & Gepp did not extend their study to include the Berlin material because they might have been able to throw some light on these discrepancies. The 'Rehm. coll.' numbers do not fit in with the series allocated to flowering plants collected at the same localities as the mosses.

REHMANN COLLECTING LOCALITIES

As previously mentioned, the main outline of Rehmann's routes may be deduced from the two maps which he published (1879, 1883). However, these maps do not show all his collecting sites, many of which are obscure. Problems in locating these sites arise largely because (a) he often used his own phonetic spelling, e.g. 'Vildshill' for Fields Hill; (b) some of the farm or local names which he used are difficult to trace or have disappeared from use; (c) due to his system of numbering specimens (or due to carelessness), some localities may be listed out of the correct sequence of his itineraries; (d) he sometimes used the farmer's name, the spelling of which may be open to question; and (e) spelling mistakes were introduced by botanical authors, such as Szyszylowicz (1887, 1888) and Engler (1883). Engler was particularly liable to distort locality names, e.g. Hantbosch, Kentbosch (for Houtbosch), Klippau (Klippan), Glandsriver (Elands River) etc.

In the absence of dates on his specimens, the only clue to the sequence of his collecting localities is provided by the numbers on his flowering plant and fern labels. However, it is apparent that he numbered his specimens in series after his return from his second visit, starting with the Cape Province and continuing with the Orange Free State, then Transvaal and finally Natal. This sequence ignores the fact that his collecting in the Transvaal took place only during his second visit, whereas the route between Ladysmith and Durban was traversed on three occasions: once during his first visit and twice during his second. It is also known that he spent a week or two in and around Cape Town on his final return voyage, when he again collected mosses and probably flowering plants as well. Certain parts of South Africa were, therefore, visited on more than one occasion, months or years apart, but this is not evident from his rotation numbers.

According to his plant numbers, it would seem that he first made a short excursion from Knysna to Montagu Pass and back. The lowest number seen is 28 (*Disa sagittalis* in Fl. Cap. 5,3: 240) from Outeniqua Mountains, where he collected over 300 numbers. Presumably he took a boat from Cape Town to Knysna and back but, in the absence of recorded dates, this could equally well have been done at the end of his first tour as at the beginning. He then collected around Cape Town (Nos 573–2219) before leaving by ox-wagon for Tulbagh, Ceres and Worcester, and then across the Karoo to Beaufort West, Victoria West, Hopetown and Kimberley. Turning eatsward, he passed through Bloemfontein, touched at the Korannaberg and reached the Caledon River near the Witteberg (north of Ficksburg) before proceeding to Bethlehem. From here his plant numbers jump to Pretoria (Nos 4018–4747), whereas the route he followed on his first visit took him from Bethlehem to Van Reenens Pass, Ladysmith, Pietermaritzburg and Durban.

On his second visit in 1879–80 he landed at Durban and travelled to Van Reenens Pass from where he made a wide sweep to Heilbron, crossed the Vaal probably at Lindeques Drift (near the present Vereeniging), kept to the east of the Witwatersrand and arrived in Pretoria probably in October 1879. There is no record of plants being collected in the eastern Orange Free State between Van Reenens Pass and Pretoria during this journey, suggesting that he may have travelled by stage coach (or, at any rate, not independently with his own transport) on this occasion.

From Pretoria, in addition to the main north road to Warmbaths, Nylstroom and Potgietersrus, there were two north-eastern wagon routes which kept to the east of the Waterberg plateau. One of these, the more easterly route, went through Derdepoort and Kameelpoort and crossed the Elands River at about Wyedrif. The other branched off at Hammanskraal, kept to the north of the Elands River and joined the eastern route at Dronkfontein (see Fig. 9), a locality feared by early travellers because of the prevalence of lions. It is apparent that Rehmann travelled along both these routes but which one on the outward and which one on the return journey is not indicated. From Dronkfontein the road crossed the Springbok Flats, where surface water was scarce, one of the most reliable perennial sources being at Klippan, situated near the present Grass Valley (Grasvallei). From here the route went through the area occupied by Chief Zebedeli's people and through Strydpoort

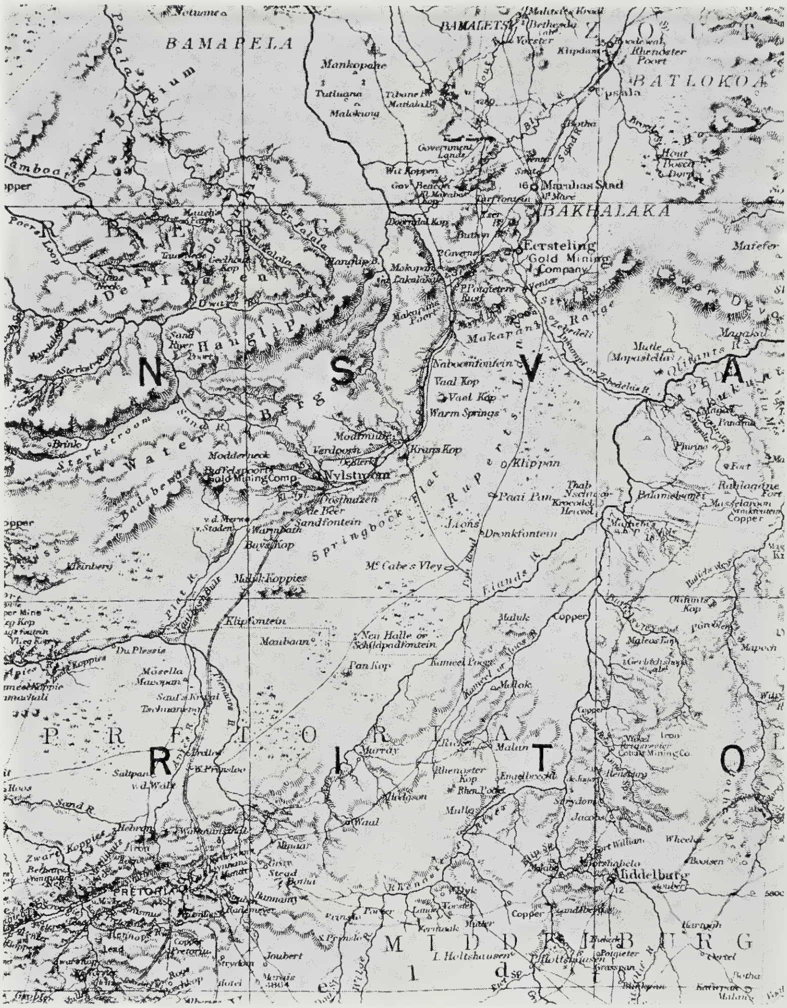


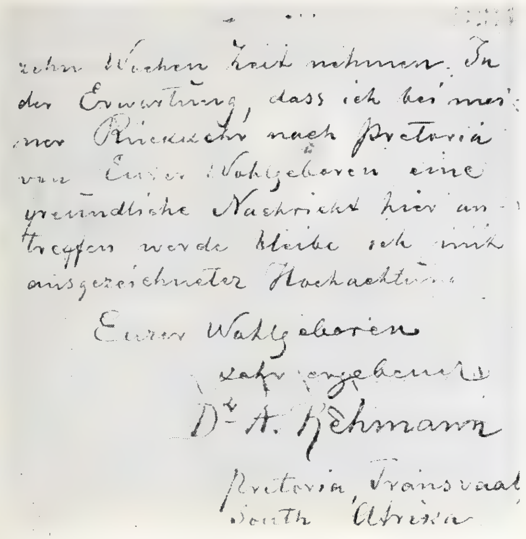
FIG. 9.—Part of Jeppe's 1: 850 000 map (London, 1879).

in the Makapaansberge to Marabastad (near the present Pietersburg). Here Rehmann turned eastward to the Houtbosch, where the forests were soon to be exploited for the growing village of Pretoria and, shortly after this, for the goldfields of the Witwatersrand.

The condition of the vegetation at Houtbosch must have been so favourable that Rehmann spent some time here, collecting about 1 000 numbers (5557–6518). He then returned to Pretoria and the next number seen was from Donkerhoek (6522), east of Pretoria on his way back to the Natal border via Standerton. His Natal numbers run from 6878–6935 at Coldstream (near Charlestown) to 7161–7181 at Colenso, after which he inserted Van Reenens Pass (visited during his first expedition) with numbers 7200–7281, before continuing to Mooi River (then known as Westown), Pietermaritzburg and Durban, the highest number seen, 9067, being recorded from Verulam.

When his localities are thus arranged according to his serial numbers, occasional discrepancies in the geographical sequence become apparent. The case of Van Reenens Pass has been mentioned, but certain other cases may be due to carelessness or because he took alternative routes between certain places. For example, Ceres occurs twice, firstly as 'Ceres Distr.: Michelspass' with numbers 2332–2347, appropriately placed between Bainskloof (2288–2328) and 'Worcester: Brandvley' (2376–2392), and secondly as 'Bokkeveld: Ceres' (3055–3095), between several Karoo localities and Beaufort West. Another discrepancy may be noted in the Orange Free State where specimens from the Korannaberg (4000–4006) are numbered after instead of before the Witteberg (3947–3992).

Doubts arising from these inconsistencies add to the difficulty in trying to locate some of Rehmann's obscure or misspelt collecting sites. Accurate dates on the specimens would have been of some assistance in verifying the sequence, but the only known case of a date being recorded on a specimen was one cited by Dixon & Gepp (1923, p.221). Moss No. 485, which is a repetition, under a different name, of No. 279, was collected 'in cavernis montium Witteberge supra Kadziberg, ad rupes. m. Aprili 1876'.



zehn Wochen Zeit nehmen. In
der Erwartung, dass ich bei mei-
ner Rückkehr nach Pretoria
von Euer Wohlgeboren eine
freundliche Nachricht hier an-
treffen werde bleibe ich mit
ausgezeichneter Hochachtung

Euer Wohlgeboren
sehr ergebener
Dr A. Rehmann

Pretoria, Transvaal
South Africa

FIG. 10.—Part of a letter from Rehmann to Kew, dated in Pretoria 1 12. 1879, by courtesy of the Director, Royal Botanic Gardens, Kew.

With regard to the second expedition, there is a letter from Rehmann preserved in the library of the Royal Botanic Gardens, Kew, dated in Pretoria 1. XII. 1879 (Fig. 10). In it he states that he had already spent seven weeks in Pretoria and had collected 500 phanerogams and 200 lichens (c. 4 000 specimens). He planned to leave two days later for the north 'über Zoutpansberge an den Limpopofluss'. His journey, of course, terminated at the Houtbosch. As already noted, in May 1880 he was in Cape Town on his return journey to Europe. The next letter received at Kew was written (in reasonably good English!) from Cracow dated 8 August 1880.

An interesting point which emerges from this correspondence is that in January 1878, shortly after his return from the first expedition, Rehmann wrote to Kew offering moss exsiccata for sale and saying that he had given up the idea of a second visit to Africa. He considered that more would be gained by going to India, Ceylon, Malaya and Borneo. He enquired if Kew would be prepared to provide some subvention, in which case he would collect living plants as well, but apparently Kew replied in the negative. The next letter to Kew was the one from Pretoria in which enquiries about financial support were repeated in order to allow him to travel from Durban to Mauritius and Madagascar before returning to Europe. Again one must assume that the response was negative because in May 1880 he was in Cape Town, where Bolus noted in his diary that he had made a loan of £24 to Rehmann.

A useful source for finding old place names is Jeppe's 1:850 000 map (London, 1879), a portion of which is reproduced in Fig. 9. Some of Rehmann's obscure Transvaal localities, such as Minaarsfarm, Neu Halle, McCabe's Vlei and Porter are shown on this map whereas others, such as Kleinsmit and Page's Hotel have still not been traced. Some localities, such as 'Axallsfarm' in the Hex River Valley, may be impossible to find at this stage, especially as the farmer's name is probably spelt wrongly. Reference may be made to Fig. 7 which shows the temporary label which he sent with his No. 80 to Engler, on which the locality is given as '5 eng. M. westlich van New Castle bei einem Farmer dessen Namen ich nicht herausfinden kann. Vielleicht ist der Name in meinen Reisebüchern enthalten?" This locality was later rendered from his standard labels for Nos 7024–7052 as 'Arnoldsfarm' and 'Arndolfsfarm' (in Szyszylowicz 1887, 1888), whereas the farmer in question was probably Adendorff, whose descendants still farm near Newcastle. This raises a question regarding the reliability of his travel diary.

Certain differences may be noted between his moss labels and those for his phanerogams and ferns, with the moss labels usually having more information, in the form of a habitat note, than is found on the flowering plant and fern labels. There are also occasional differences in the presentation of locality information. For example 'Natal: Drakensberg Van Reenenspass' is recorded on flowering plant labels, whereas on mosses it is rendered as 'Natal: Kwatlamba ad Van Reenen's Pass'. Kwatlamba or Quatlamba was the original native name for the Drakensberg range. On the specimens collected in the Woodbush area of the Transvaal, the flowering plants bear simply the locality 'Houtbosh', whereas on the moss labels more details are given, such as 'mont. Lechlaba ad Houtbosch', 'Lechlaba supra locum Mamabolo' and 'Lechlaba, Snellskop'. Lechlaba appears to be the range also referred to as Houtboschberg, on which Schneleskop, at over 2 000 m above sea level, is the highest peak, and which separates the source of the Letaba River from the Broederstroom (Rehmann 1883, p. 376). Rehmann no doubt made his headquarters at the Berlin Mission Station which was established on this range at Mphome in 1878 (Fig. 11). In February 1894 Rudolph Schlechter also visited the Station and shortly afterwards, in 1896, it was moved to a lower and more congenial site at Krantzenstein, near the present Houtboschdorp.

In the list of Rehmann collecting sites in Table 1, the place names are first given as they are spelt on the labels or in literature. These are followed, where necessary, by the present-day spellings and locations mainly according to Southern African Place Names by Leistner & Morris (1976). In certain cases farm names have been found on the Trig. Survey 1: 250 000 Topocadastral series and these are indicated by (TC). The collecting numbers refer only to phanerogams and ferns and were derived from various literature sources. The numbers for mosses are not listed, because they convey no information on the sequence of localities in the route followed.

As mentioned earlier, Rehmann's personal set of African phanerogams and ferns is in Z. Good sets are also in BM, BOL, BR and K. The types of some species described by Engler may be in B, for example *Zantedeschia macrocarpa* Engl., though no material of *Z. rehmannii* Engl. appears to have been retained by him. According to 'The history of the collections contained in the Natural History Depart-

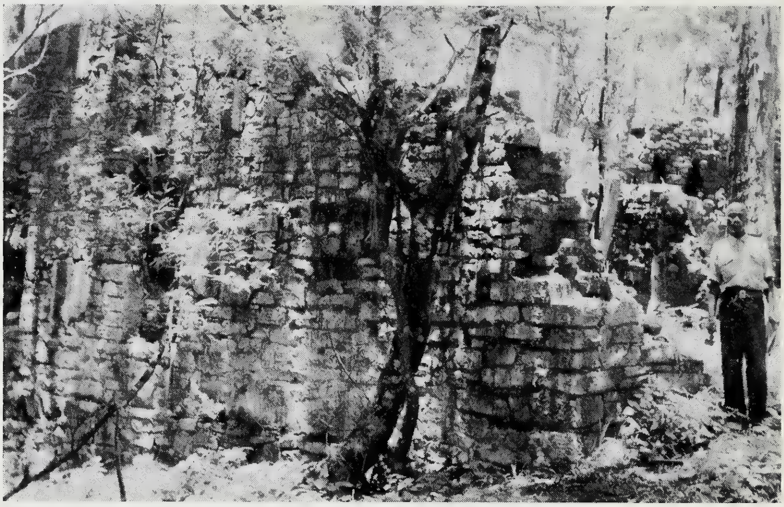


FIG. 11.—Ruins of the Mphome Mission Station, Houtboschberg, taken in 1956.

TABLE 1.—Rehmann's collecting numbers with the localities as spelt by Rehmann, the present day spelling, occasional notes and the grid reference

Collecting numbers	Region, 'district' or province	Collecting locality as spelt by Rehmann	Collecting locality as spelt today with notes	Grid reference
28—340 (also moses)	Outeniqua Mountains	Montagu Pass		3322CD
354—367 (also mosses)	Knysna District	Portland	7 km NW of Knysna	3322DD
398—478 (also mosses)	do	Belveder	Belvidere, the home of Capt. T.H. Duthie	3422BB
486—504 (also mosses)	do	Esternek, Esterneck	Probably a corruption of Yzernek, 5 km NE of Knysna	3323CC
mosses only	do	In silvis Knysnae		
555—563 (also mosses)	George Town District	Oakfort	Probably should be Oakhurst, the residence of the Dumbletons, about 25 km E of George. W.D. Dumbleton sent a *Gladiolus* specimen to Kew in 1870 which was named *G. splendens* Bak.	3322DD
mosses only	do	Blanco		3322CD
mosses only	do	Towriver	Touw (or Touws) River enters the sea near the Wilderness at Fairy Knowe, where W.D. Dumbleton also had a property	3322DC
573—840 (also mosses)	Promontorium Bonae Spei	in monte Tabulari	Table Mountain	3318CD
977—1175 (also mosses)	do	in monte Diaboli	Devils Peak	3318CD
1118—1382 (also mosses)	do	Cape Town, Stinkwater	Blinkwater	3318CD
1412—1553	do	Cape Town and Cape Flats		3318DC/ 3418BA
mosses only	do	Lionshead and Greenpoint		3318CD
1588—1603 (also mosses)	do	Camps Bay		3318CD
1609—1632 (also mosses)	do	Hout Bay		3418AB
1650—1729 (also mosses)	do	Rondebosch		3318CD
mosses only	do	Newlands and Clermont	Claremont	3318CD

TABLE 1. **Continued**

Collecting numbers	Region, 'district' or province	Collecting locality as spelt by Rehmann	Collecting locality as spelt today with notes	Grid reference
1829—2219	do	Cape Flats		3318DC/ 3418BA
2238—2256	Drakenstein Berge	Tulbagh		3319AC
2267	do	Klapmuth	Probably should be Klapmuts	3318DD
2270 (also mosses)	do	Wellington		3318DB
2288—2328	do	Bainskloof		3319CA
2332—2347	Ceres District	Michelspass	Michells Pass	3319AD
2376—2433	Worcester District	Brandvley, Brandvaley	Brandvlei	3319CB
2451—2590 (also mosses)	do	In montibus supra Worcester		3319CB
2711—2729 (also mosses)	Hexriverberge	Axallsfarm, Axellsfarm	Not found	probably 3319DA
2772—2776	Worcester District	Hexrivervalley, Groote Tafelberg	It is not certain which Tafelberg is meant as there are several possibilities. The most likely is one shown on old maps which appears to be near the Oliviersberg but this is not in the Hex River Valley. If his sequence is correct it would be a mountain near Verkeerde Vlei, which would point to the Bonteberg	3220CD 3319BD
2833—2852	Karroo	Verkeerde Valley	Verkeerde Vlei	3319BD
2910—2952	do	Witteberge, Maggisfontein	Probably Matjiesfontein but this again would be out of sequence	3320BA
2975—2994	Koup	Flakkraal	Probably the farm Vlakkraal (TC) just north of Prince Albert Road. The Koup (from the Hottentot word for the abdominal fat of the ox) is the arid, barren area south of the Nuweveldberg and west of Beaufort West, and is the upper catchment of the Dwyka and Gamka Rivers	3221DC
3003—3014 and 3050	Karroo	Grootfontein	Probably the farm Grootfontein (TC) on which Koup railway station is now situated	3321AB
3034	do	Potatosriver	Also Patatsrivier	3320AB
3033, 3041	do	Draaikop	Probably Driekop, near Potatos River	3320AB
3055—3095	Bokkeveld	Ceres	It will be noted that the geographical sequence is erratic between Nos 2332 and 3131 probably because he made two journeys, along different routes, between Ceres and Matjiesfontein (see Fig. 2)	3319AD
mosses only	do	Lionsfontein	Probably the farm Leeuwfontein (TC), 22 km NE of Ceres	3319AD
mosses only	Karroo	ad rip. flum. Gamkoo	Gamka River. His route would have met the Gamka River south of Fraserburg Road	3221DD

TABLE 1. **Continued**

Collecting numbers	Region, 'district' or province	Collecting locality as spelt by Rehmann	Collecting locality as spelt today with notes	Grid reference
3131—3157	Roggeveld	Beaufort	Beaufort West	3222BC
3177—3178	do	Rhenosterkop	Renosterkop	3222BB
3180—3185	do	Korlanskloof	This is no doubt the farm Courlands Kloof (TC), just to the W of Nelspoort	3222BB
3198—3205	do	inter Salt- et Brakriver	This covers a distance of over 100 km on the road between Nelspoort and about 25 km N of Victoria West	3222BB/ 3123AA
3219	do	Victoria	Victoria West	3123AC
3220—3223	do	Hopetown		2924CA
3243—3269	do	Rietpoort	Probably the farm Rietpoort (TC), on the Brak River 25 km N of Victoria West though this is out of sequence	3123AA
3279—3281	do	Kopisdam, Kapisdam	Probably a corruption of Koppiesdam. There are several farms with this name (or variations of it) not far from Rehmann's route, e.g. Koppies Dam ca. 18 km W of Strydenburg Kopjesdam ca. 42 km E of Hopetown (2924CB) and Koppies Dam 20 km SW of Kimberley (2824DC). The last-mentioned seems the most likely but it is out of sequence	(2923CD)
3346—3355	Griqualand West	Eitalersfontein	No such place can be found	
3380—3394	do	Hünernestkloof	Heuningneskloof	2924BA
3407—3428	do	Junction	This probably refers to the junction of the Modder and Riet Rivers	2924BA
3433—3470	do	Kimberley		2824DB
3483—3538	Orange Free State	Olifantsfontein	The farm Olifantsfontein (TC), 16 km SE of Kimberley	2824DD
3544—3567	do	Kanonfontein	Not found	
3573—3610	do	Mudriverdrift	No doubt where the Kimberley-Bloemfontein road crosses the Modder River ca. 45 km SE of Kimberley	2825CC
3622—3676	do	Drainfontein	Could be a corruption of Draaifontein but, even so, no place name resembling this has been found along Rehmann's route in the O.F.S.	
3688—3735	do	Rietfontein	Probably the farm Rietfontein (TC), 7 km E of Petrusburg	2925AB
3762—3906 (also mosses)	do	Bloemfontein		2926AA
mosses only	do	Molmonspruit	Moolmansspruit	2827DD
3947	do	Witteberge ad Caledonriver		2828CA
3981—3999 (also mosses)	do	Witteberge, Kadziberg.	No doubt this is the Catjasberg (also spelt Katjesberg) about 6 km E of Generaalsnek and near to the Caledon River. It is on the dividing line between grid 2828CA and 2828CC	

TABLE 1. **Continued**

Collecting numbers	Region, 'district' or province	Collecting locality as spelt by Rehmann	Collecting locality as spelt today with notes	Grid reference
4000—4006	do	Korannaberg		2827CD
mosses only	do	Liebenbergsvley	Liebenbergsvlei, near Bethlehem	2828AB
mosses only	do	Bethlehem		2828AB
4018—42	Transvaal	Pretoria, Aapiespoort	This is the area now referred to as the Fountains Valley	2528CA
4341—4382	do	Pretoria, colles supra Aapiesriver	Hills above Apies River	2528CA
4471—4590	do	Pretoria, Wonderboompoort		2528CA
4627—4698	do	Pretoria, Kuduspoort	Koedoespoort	2528CB
4706—4747	do	Pretoria		2528CA
4759	do	Bosh Veld, Buchenhouts Kloof Spruit	Boekenhoutskloof. If the number is correct (Fl. Cap. 4,2:436) it is out of geographical sequence	2528CB
4784	do	Pretoria, Derde Poort		2528CB
4790	do	Bosh Veld, Pinaasriver	Pienaars River	2528CB
4801—4822	do	Bosh Veld, inter Kameelpoort et Elandsriver		2528BB
4825—4829	do	Bosh Veld, Kameelpoort		2528BD
4835—4844	do	Elandsriver, Kleinsmit	Not located.	Probably 2528BB
4851—4882	do	Bosh Veld, Menaarsfarm	See Fig. 9. Carl Minnaar's farm was evidently a recognized stopping place on the 'eastern' road to the north across the Springbok Flats. Baines (1877) places it about 26 km NE of Pretoria. It will be noted that the geographical sequence between Nos 4759 and 4999 is rather erratic, possibly because Rehmann travelled through twice, on his outward and homeward journeys	2528CB
4883—4913	do	Bosh Veld, Elandsriver, Neu Halle	Just north of Skilpadfontein in Mabaan's Location (see Fig. 9)	2528BB
4931—4999	do	Bosh Veld, Elandsriver and drift		2528BB
s.n.	do	Bosh Veld, McCabe's Vley	See Fig. 9. Near the railway siding McCabes Vlei. The name is no doubt derived from the nearby farm Makeepsvley 1134 (TC)	2429CC
5015—5154	do	Bosh Veld, inter Elandsriver et Klippan		2528BB/ 2429CB
5201—5369	do	Bosh Veld, Klippan	Situated on the farm Doornpoort 520 (TC) adjoining the farm Grass Valley (Grasvallei) This was a fairly reliable source of water on the old wagon road across the Springbok Flats	2429CB
5374—5556	do	Makapansberge, Streydpoort	Strydpoort, N. of Zebediela	2429AB

TABLE 1. **Continued**

Collecting numbers	Region, 'district' or province	Collecting locality as spelt by Rehmann	Collecting locality as spelt today with notes	Grid reference
5557—6518	do	Houtbosh	Houtboschberg At that time the Berlin Mission Station was situated on the farm Mphome 1906 (TC)	2329DD
mosses only	do	In mont. Lechlaba ad Houtbosh	Houtboschberg	2329DD
mosses only	do	In mont. Lechlaba supra Mamabolo	Houtboschberg, adjoining Mamabolo's Location	2329DD
mosses only	do	Lechlaba, Snellskop	Schneleskop is the highest point on the Houtboschberg	2329DD
6522—6552	do	Hogge Veld, Doukershoek	Donkerhoek, Donkerpoort 30 km E of Pretoria	2528CD
6571—6678	do	Hogge Veld, Bronkerspruit, Bronkersprint	Bronkhorstspruit	2528DC
6584	do	Hogge Veld, Wilgeriv. ad Porter	See Fig. 9	2528DD
6597—6658	do	Hogge Veld, inter Porter et Trigardsfontein.		2528DD/ 2629AC
6670—6731	do	Hogge Veld, Trichardsfontein	Now Trichardt, situated on the farm Trigardsfontein (TC)	2629AC
6735—6781	do	Hogge Veld, inter Trichardsfontein et Standarton		2629AC/ 2629CC
6788—6827	do	Hogge Veld, Standarton	Standerton	2629CC
6837—6842	do	Hogge Veld, Perekopberg	Perdekop	2729BA
6847—6864	do	Hogge Veld, Pages Hôtel	Not located.	Probably 2729BA
6869—6870	do	Hogge Veld, Sandspruit		2729BD
6878—6935	Natal	Drakensberg, Goldstream, Coldstream	Coldstream, 2 km N of Charlestown	2729BD
6939—6961	do	Drakensberg, Laingsnek		2729BD
mosses only	do	In mont. Kwatlamba ad Laingsnek	Drakensberg, Laingsnek	2729BD
mosses only	do	Kwatlamba, Madziuba	Drakensberg, Majuba	2729BD
6962—7009	do	Drakensberg, Mountainprospect	Mt Prospect	2729DB
7016	do	Drakensberg, Ingagane	(Fl. Cap. 5, 1:242). There is a stream by this name in grid 2829CA, but this area was not visited by Rehmann. It is probable that Ingogo (2729DB) was intended	
7029—7052	do	Drakensberg, Arndolfsfarm, Arnoldsfarm, New Castle	8 km W of Newcastle (see Fig. 7). The farmer referred to was probably Adendorff, whose descendants still farm near Newcastle	2729DD
7053—7116	do	Drakensberg, Biggarsberg		2829BB
7126—7136 (also mosses)	do	Ladysmith		2829BB
7161—7181	do	Drakensberg, Tugelariver, Colenso		2829DB
7200—7281	do	Drakensberg, Van Reenenspass		2829AD
mosses only	do	In montibus Kwatlamba ad Van Reenen's Pass		2829AD

TABLE 1. **Continued**

Collecting numbers	Region, 'district' or province	Collecting locality as spelt by Rehmann	Collecting locality as spelt today with notes	Grid reference
7297—7323	do	Griffingshill, Eastcourt.	Griffins Hill Estcourt	2929BB
7348—7352	do	Westtown, Mooiriver	Mooi River, previously known as Westtown	2929BB
7359—7404 (also mosses)	do	Karkloof		2930AC
7429—7442	do	Umgeni ad catarrhactam	Umgeni or Howick Falls	2930AC
mosses only	do	Umgeni supra Maritzburg	Probably Howick	2930AC
7491—7612	do	Maritzburg	Pietermaritzburg	2930CB
7640—7650	do	Umsondusriver	Umsunduze (Umsundusi) River	2930CB
7659—7683	do	Farkkop	Probably Vaalkop, shown on old maps near Camperdown	2930DA
7690—7803	do	Camperdown		2930DA
7871—7938 (also mosses)	do	Intschanga, Inczanga	Inchanga	2930DA
7991—8032 (also mosses)	do	Vildshill, Pinetown	Fields Hill	2930DD
8033—8072	do	Inter Pintown et Umbilo	Pinetown	2930DD
8090—8170	do	Umbilo ad catarrhactam		2930DD
8173—8404 (also mosses)	do	Inanda		2930DB
8428—8544 (also mosses)	do	Oakfort, Umhlotiriver	Oakford, shown on old maps on the Umdloti (Umhloti) River, about 12 km from the sea. Medley Wood also collected here (see Fl. Cap. 5,1:50)	2931CA
8580—9057	do	Durban and Umgeni		2931CC
9064—9067	do	Verulam		2931CA

ments of the British Museum', London (1904), 2 176 phanerogams specimens and 1 293 cryptogams were purchased from Rehmann by the British Museum between 1881 and 1890. The Kew set, according to Jackson (1901), includes specimens from South Africa and Europe and consists of over 2 887 specimens acquired between 1878 and 1898. It is known from the correspondence preserved at Kew that an offer of 500–600 South African mosses was received from Rehmann in January 1878, while the receipt of 1766 phanerogams was acknowledged in 1882. There is a list of the latter at Kew in N. E. Brown's handwriting but unfortunately no localities are recorded. The Kew moss herbarium has, of course, been transferred to BM. There are about 800 Rehmann phanerogams in BR, between Nos 1 and 2 100, acquired towards the end of the 19th or beginning of the 20th century. Types of grasses described by Hackel, including several Rehmann specimens, were seen in W by Schweickerdt when he studied the genus *Aristida* for his revision in Bothalia 4: 91–175 (1941), but no reply regarding their present holdings has been received. It is, however, known that they have a specimen of *Greyia radlkoferi* Szyszyl., annotated by Szyszylowicz and presumably the holotype, and they may have others.

He is commemorated in the moss genus *Rehmaniella* C. Müll. and in a great many species names, including *Triaspis rehmannii* Szyszyl., *Ochna rehmannii* Szyszyl., *Rhus rehmanniana* Engl., *Commiphora rehmannii* Engl., *Acacia rehmanniana* Schinz, *Coleus rehmannii* Briq., *Plectranthus rehmannii* Gürke, *Stachys rehmannii* Skan, *Selago rehmannii* Rolfe etc.

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UITTREKSEL

Anton Rehmann het gedurende die jare 1875–77 en 1879–80 twee versamelingstogte orderneem. In dié tydperk het hy meer as 9 000 nommers versamel. Met die laaste reis het hy so ver noord as Houtbosch in Transvaal gevorder, waar hy die eerste was om 'n ekstensiewe versameling te maak. 'n Kort verslag oor sy lewe en reisplanne in Suid-Afrika word gegee, met besonderhede van versamelingslokaliteite waar moontlik.

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* Efforts have been made to establish the dates with greater precision, but it has not been possible to establish more than the years of publication.

Bothalia 14,1: 15–26 (1982)

Notes on the genus *Ficinia* (Cyperaceae): morphological variation within the section *Bracteosae*

T.H. ARNOLD* and K.D. GORDON-GRAY**

ABSTRACT

Generic limits of *Ficinia* are reviewed. Morphological variation within the section *Bracteosae* Pfeiff. of *Ficinia* Schrad. (Cyperaceae) is examined and discussed. Diagnostic characters previously in use in classification are reviewed together with a number of new characters. These have enabled the limits of many existing taxa to be refined, and have provided the basis for the establishment of a number of new taxa recently described. Characters examined include: underground organs, leaf sheaths and ligules, leaf blades, inflorescence structure, prophylls, styles, anthers, achenes, gynophores and inflorescence axes.

INTRODUCTION

This paper is the second in a series on *Ficinia*. In the first (Arnold & Gordon-Gray, 1978) nine new taxa belonging to the section *Bracteosae* are described. In this paper morphological variations within the section are discussed, and will be followed by part three of the series in which a detailed account of the taxonomy, nomenclature and distribution of taxa in the section *Bracteosae* will be presented.

The major genera of the tribe *Scirpeae,* with the exception of *Ficinia* and to a lesser extent *Eleocharis,* have come under close scrutiny in recent years. *Scirpus* L., long considered unnatural, has been studied by a succession of workers including Beetle (1940; 1944 & 1945), Koyama (1961), Schultze-Motel (1971), Schuyler (1971) and Oteng-Yeboah (1974) and is still receiving attention. *Fimbristylis* Vahl and *Bulbostylis* Kunth have likewise been the subject of some degree of investigation, especially the African species (Gordon-Gray, 1965, 1971; Lye, 1971, 1973). The South African species of *Fuirena* are at present under revision (Forbes, pers. comm.) Koyama (1961) would include *Fuirena* in *Scirpus. Eleocharis* has been the subject of studies particularly in America (Harms, 1968, 1972), (Strandhede, 1967), (Svenson, 1939, 1947), but its African, especially South African, species are not adequately known. *Ficinia* is also placed within *Scirpeae.* Apart from studies of this genus for inclusion in regional floras (Clarke, 1898; Levyns, 1950) the most recent comprehensive investigation into the genus has been that of Pfeiffer (1920) at a time when generic limits were not so much in question as they are now.

At least 132 species have been described within the genus *Ficinia*, but of these only 55 to 60 appear to be good species, the rest having been relegated to synonymy. The majority of these species are endemic to South Africa, more especially its southern and south-western regions. One south-western species, *F. nigrescens (=F. bracteata),* extends to South West Africa / Namibia (Podlech, 1967). Of the remaining species that exceed the boundaries of South Africa, two reach Mount Kilimanjaro (Clarke, 1898) but are also South African, two are recorded from Abyssinia, one of which is endemic there, whereas the other occurs in South Africa. The Abyssinian endemic, *F. clandestina,* is considered by Arnold & Gordon-Gray (1978) not to belong to *Ficinia:* its correct generic status is uncertain. Five extra-African species of *Ficinia* have been recorded, three are from the Malagasy Republic (Chermezon, 1937) and two, *F. indica* Lam. and *F. foliacea-bracteata* Pfeiff. were reported from the East Indies (Java). Raynal (1958) has shown that the last-named entity is not a species of *Ficinia* but rather *Cyperus cephalotes* Vahl, and it will be shown in a paper to follow that Lamarck's type of *F. indica,* collected by Sonnerat, is almost certainly from the Cape of Good Hope rather than from the East Indies. This means that, apart from three species in Malagasy, the genus is exclusively African, being predominantly southern and temperate, but extending northwards along mountain ridges into the eastern Cape, Natal, the Transvaal, Zimbabwe and the mountains of Kenya and Abyssinia. There are certainly undescribed species of *Ficinia* in eastern South Africa and presumably others in the rest of South Africa and Zimbabwe. These, however, will not be dealt with here, for the present study covers only the section *Bracteosae* which is confined in natural distribution to the south-eastern, south-western and western Cape from East London to the border of South West Africa and inland as far as Grahamstown, Graaff Reinet, Montagu and Clanwilliam. This section, according to Pfeiffer's 1920 classification, belongs to the subgenus *Eu-Ficinia,* comprises three subsections. Of these *Sickmannia* and *Arboriculmes* are each monotypic, with the third subsection, Seticulmes, comprising ten species.

Within *Ficinia* there are a number of individual species, and species groups that, in the past, have been used as 'dumping grounds' for plants difficult to identify. The largest and perhaps the most problematic of these groups is the *F. indica*/ *F.pallens* complex which forms the major part of the section *Bracteosae.* All who have studied this complex have treated it differently. At one extreme its component taxa have been regarded as varieties

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of a single species (Schonland, 1922), whereas at the other extreme five distinct species are recognized (Levyns, 1950). None of the work carried out so far has been entirely satisfactory and, if anything, has tended to compound rather than to clarify the confusion.

In the present investigation, morphological variation is examined in the hope that this will clarify some of the taxonomic, distributional and nomenclatural problems existing in the section *Bracteosae* with special attention being focused upon the *F. indica*/*F. pallens* complex.

GENERIC LIMITS OF *FICINIA*

Within the tribe *Scirpeae, Ficinia* is most closely allied to the genus *Scirpus* and more especially to the section *Isolepis* of this genus. Before *Ficinia* was established, many of the species now assigned to it were included in this section. Species of *Ficinia* may be distinguished from it, however, by their possession of a small, obconical, pedicellike structure or gynophore (also referred to as a discus) responsible for elevating the achene above the receptacle.

According to C.B. Clarke (1898) it is difficult to attribute very much importance to this structure, because it is difficult to draw the line between it and the expanded foot associated with the achene of many species of *Scirpus,* therefore *Ficinia pulchella* of Kunth is *Scirpus pulchella* Boeck. Furthermore, a small gynophore is also present in some species of Fimbristylis, and varies greatly in development in one of the species in this genus, namely, *F. ferruginea* (L.) Vahl.

Schonland (1922) draws attention to the fact that an obpyramidal small stalk which becomes detached with the nut, besides being present in species of *Scirpus* and *Fimbristylis* is also found in *Scleria* and *Diplacrum* of the tribe *Rhynchosporae.* The main difference, however, between these genera and *Ficinia* lies in there being a small lobed somewhat fleshy outgrowth surrounding the base of the ovary in *Ficinia* and that this structure is normally three-lobed or has three main lobes.

The present investigation has shown these observations to be accurate, for all the taxa studied possessed an out-growth or outgrowths from the apex of the gynophore which enveloped all or part of the lower portion of the nut. The form of the outgrowth is highly variable within the genus, ranging from a cup-like structure to 2–3 lobes generally joined near their bases.

The use of the gynophore as the solitary attribute characterizing the genus *Ficinia* has, for the greater part, been successful in uniting a large, relatively heterogeneous group of plants, which in the past were considered by some workers to comprise a number of distinct genera.

Ficinia includes a number of taxa with nuts that lack a gynophore. Among these are *F. tenuifolia* Kunth and *F. rigida* Levyns. Because of the 'ficinioid facies' of these plants, it has been generally accepted that they be included in *Ficinia. Scirpus falsus* C.B. Cl. and *Scirpus ficiniodes* Kunth, on the other hand (to be dealt with in some detail in a separate paper), despite their 'ficinioid' appearance, have been placed in *Scirpus,* but not without recognition of the uncertainty of this relationship, reflected as it is, in their specific epithets. The two major attributes which dictated their inclusion in *Scirpus* were, firstly, the lack of a gynophore, and, secondly, the presence of six bristles surrounding each flower, a feature unrepresented in *Ficinia,* but characteristic of certain members of *Scirpus.* Therefore it is evident that the boundary between *Scirpus* and *Ficinia* is by no means clearcut nor well defined.

The 'ficinioid' appearance already mentioned is the cumulative effect of a number of minor features exhibited by a large number of species, particularly those of the section *Bracteosae.* It is a means by which plants of the genus can usually be distinguished quite readily from species of allied genera, often on superficial inspection alone.

The characters which collectively give this 'ficinioid facies' are the erect, and sometimes rigid, leaf blades that are often almost cylindric and stem-like rather than flattened and leaf-like; the membranous or scarious leaf sheaths that in many instances are prolonged upwards into definite ligules, the often (but not always) condensed and highly compacted obovate to elliptical inflorescences enveloped almost completely, or only partially, in an involucre formed by the dilated bases of the outer bracts, the longitudinally striated appearance and, often, the hard, brittle texture of these bracts and sometimes of the smaller glumes within them.

This 'ficinioid facies' is not commonly exhibited by members of the section *Isolepiformes,* which closely resemble *Scirpus,* and it is a typical of the subgenus *Hemichlaena* in which the glumes are distichously ranked and the spikelets compressed.

This strongly suggests that present generic limits, defined almost exclusively as they are by the presence of a gynophore beneath the achene, are artificial, unnatural and probably too wide. There is, therefore, an important need to re-examine all species with a view to determining critical, and especially new, criteria that will effectively delimit natural groups within the genus.

DIAGNOSTIC CHARACTERS EXHIBITED BY THE SECTION *BRACTEOSAE*

The characters selected by past workers to delineate the different taxa within *Ficinia* have not always been entirely successful in fulfilling this function. Many, with use, have proved to exhibit a considerable range in variation, extending beyond the limits originally intended for them, and are therefore considered to be unreliable.

Many taxa at their establishment were inadequately defined by too few characters. With time, and under the interpretation of numerous workers, these taxa have become heterogeneous, so that on more careful scrutiny and with the application of more critical diagnostic criteria they fell, during the present work, into relatively homogeneous sub-units worthy of independent recognition sometimes at specific, sometimes at infraspecific levels.

New characters and others previously in use that require special consideration are dealt with in sequence beginning with vegetative organs and proceeding to reproductive structures.

Underground organs

Growth is sympodial in all the taxa studied. In this sense all plants possess a rhizome, for even in the compactly tufted plants, a very abbreviated rhizome links successive shoots together.

Previous workers have made reference to the presence of stolons in some taxa of the section *Bracteosae* and their absence in others. These 'stolons' are essentially rhizomes, for they are underground stems clothed in leaf scales, but they are markedly elongated in comparison with the rhizomes developed in the more or less compactly tufted plants. Each gives rise to a new plant at its tip and thus the term 'stolon' is correctly applied to them (Lawrence, 1951, Willis, 1973). Two main rhizome forms, which differ in degree of development rather than basic structure, are represented in the section *Bracteosae* (Fig. 1).

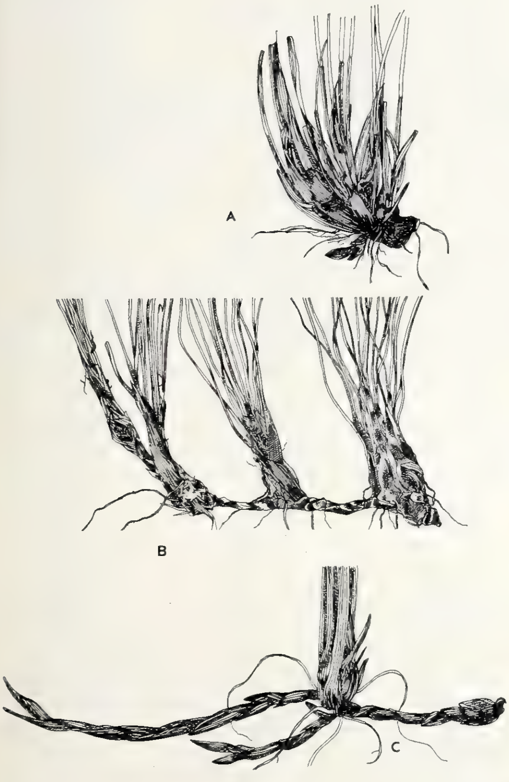

FIG. 1.—Rhizomes: A, rhizome very short, plants compactly tufted e.g. *F. capitella;* B, rhizome shortly elongate plants loosely tufted e.g. *F. pallens* var. *pallens;* C, rhizome elongate, plants stoloniferous e.g. *F. indica* (all natural size).

(i) Abbreviated rhizomes

Many of the taxa studied possessed abbreviated rhizomes but these, despite their short length, were not uniform. They fell into two subgroups. Little variation occurred within the first. Here the rhizome did not exceed 2–3 mm in length. It is inconspicuous except when innovations are developed, being concealed by persistent leaf basis.

The rhizomes of successive shoots are very closely packed resulting in the development of plants with compactly tufted growth forms (Fig. 1A) for example *F. capitella.*

The second subgroup comprises plants in which the rhizome structure is more variable in length. Here it ranges from 2–25 mm and is either uniform in width or swollen apically, as in *F. pallens* var. *pallens,* to form a tuberous base to the aerial shoot. (Fig. 1B).

The rhizomes are clothed in short, obtuse, striate scale bracts that are usually persistent, for example *F. levynsiae.* Plants falling within this second subgroup, because of their less abbreviated rhizomes, develop a loosely tufted growth form, that, in its most extreme expression, is distinct from the compactly tufted growth form illustrated in Fig. 1A. Gradation occurred between the two forms, however, depending upon the length of the rhizome and the number of shoots developed in proximity to one another.

(ii) *Elongated rhizomes*

Here rhizome structure is relatively uniform. Some variation in length occurs, but all rhizomes are clearly well developed and elongated up to 150 mm in length. They are more or less uniform in width and clothed in linear-acuminate, striate, pale brown to yellow scale bracts that are persistent for the most part, but which in some taxa are lost as the rhizome became shrunken and wiry with age (Fig. 1C). Plants with elongated rhizomes have been described in the present study as stoloniferous, for example, *F. dunensis.*

Rhizome structure and growth form are useful in distinguishing some taxa (especially in the field). In the herbarium compactly tufted plants can only be differentiated from stoloniferous plants if stolons are included in the specimen.

Two species, *F. dunensis* and *F. pallens,* show variation in the development, or not, of stolons. *F. dunensis,* plants growing on sand dunes near the coast, regularly produce stolons that are usually represented on herbarium sheets. Plants from inland are compactly tufted with no evidence of elongated underground stolons. This difference may be attributed to the different habitat conditions under which the plants grow, as *F. dunensis* is a widely distributed species. In *F. pallens,* stolons are present only in var. *pallens,* distributed along the Cape Peninsula. In var. *lithosperma* from the Caledon area, no stolons have been recorded. This lack of stolons may be linked to the dry climatic conditions in this area as opposed to the wetter conditions that prevail along the Peninsula. Plants of var. *lithosperma* are compactly tufted, more rigid and have

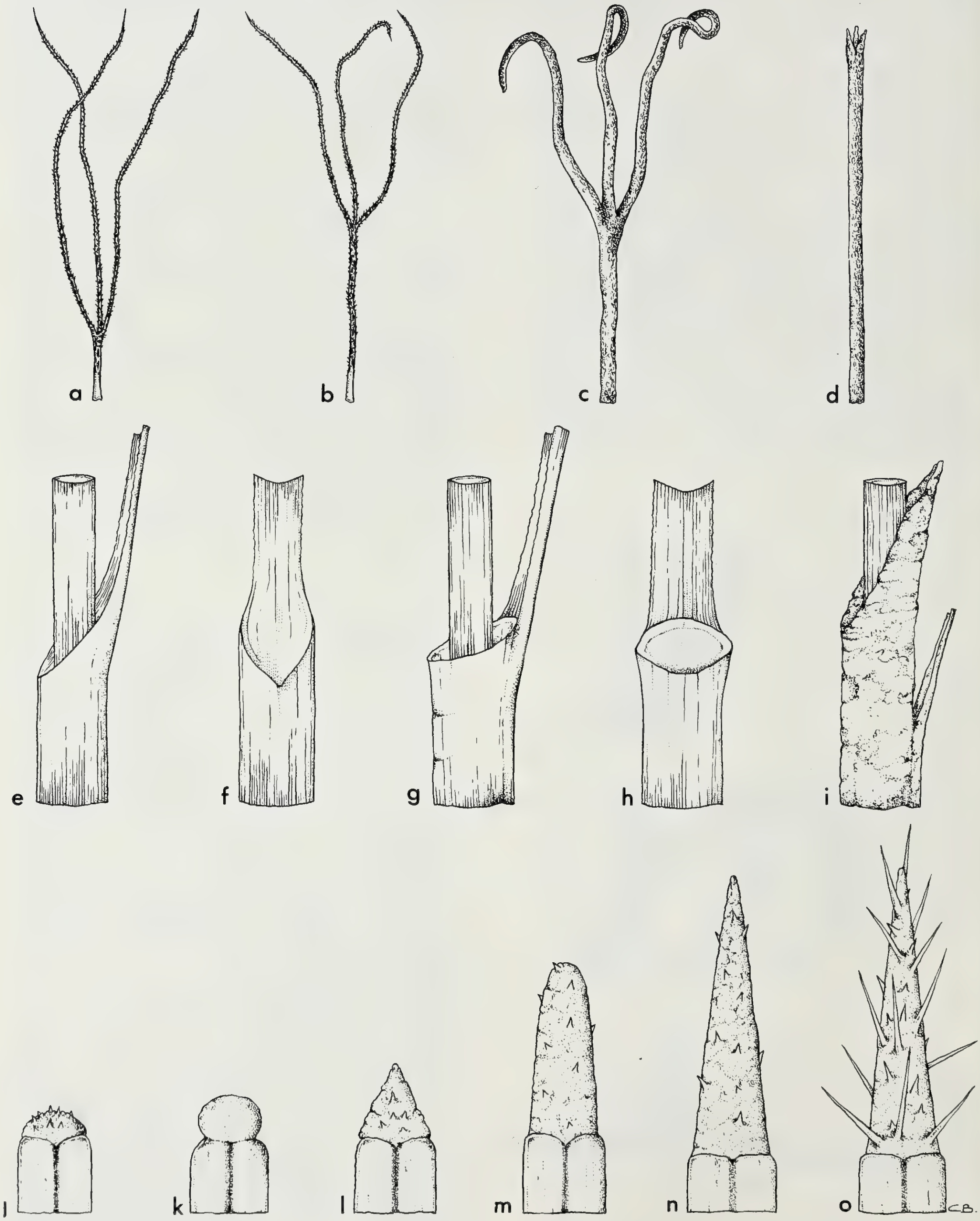

FIG. 2. — Styles and branches a-d (× 11); leaf sheaths and ligules, e-i (× 7); anther crests j-o (× 50). a, *F. arenicola* var. *arenicola;* b, *F. ixioides;* c, *F. cedarbergensis;* d, *F. radiata;* e & f, *F. latifolia;* g & h, *F. nigrescens;* i, *deusta;* j, *F. petrophylla;* k, *F. grandiflora;* l, *F. levynsiae;* m, *F. arenicola;* n, *F. ixioides* subsp. *glabra;* o, *F. ixioides* subsp, *ixioides.*

distinctly harder inflorescence bracts than plants of var. *pallens*.

This is suggestive of adaptation to drier conditions. It is also possible that the presence or absence of stolons is to some extent genetically controlled, as the two varieties are, for the most part, allopatric in distribution, and could therefore represent independent gene pools.

Leaf sheaths and ligules

Two distinct types of leaf sheath are represented among the taxa studied. The first of these is membranous, usually transparent or pale brown to red, glabrous and splitting longitudinally with age. Such leaf sheaths are eligulate, or carry very short inconspicuous ligules that seldom exceeded 3 mm in length. In the eligulate forms the membranous sheath-tissue is joined to the two margins of the thicker sheath tissue that, when extended, formed the leaf blade. Therefore the membranous tissue does not extend across the inner surface of the leaf blade, for example, *F. radiata* and *F. latifolia* (Fig. 2e & f). In the ligulate forms this membranous portion of the sheath extends across the inner surface of the blade to form a complete cylinder, for example *F. arenicola* and *F. nigrescens* (Fig. 2g & h). The sheath apices of the eligulate forms are oblique, whereas those of the ligulate forms are more often truncate.

The second type of leaf sheath is markedly scarious or papery, wrinkled, fragile and white or greyish, and generally flecked with brown markings, for example, *F. deusta* (Fig. 2i). In this sheath type the ligule is always well developed and up to 3 cm in length in some taxa. The ligule apices, although commonly oblique, are sometimes suboblique two-lobed, or occasionally truncate. This variation occurs not only among taxa, but within them, so that as a diagnostic character the shape of the sheath apex of this second type is unreliable. It is often difficult to distinguish the original form of the stem apex because the scarious tissue, being very delicate, tears and splits easily, giving rise to a ragged, conspicuous, but uninterpretable mass of tissue near the apex of the shoot. Despite this, the two clearly different types of sheath are useful in the separation of some taxa.

Leaf blades

Most of the taxa in *Ficinia* exhibit well developed leaf blades. Only in a few taxa are elongate leaf blades absent, in the section *Bracteosae* this condition is exhibited only by *F. gydomontana*.

Leaf blade length, although not a completely reliable character in most species, is useful in distinguishing *F. petraphylla* and *F. arenicola* from other species of the section. In these two taxa the blades are characteristically longer than the culms.

Considerable variation exists in the presence and degree of development of the leaf margins. In some taxa the blades are flat, with well defined margins: in others the margins are scarcely or not represented since the blades are cylindrical. Between these extremes a complete range occurs.

Metcalfe (1970) correlated the degree of infolding of the leaf margins with environmental conditions, regarding infolding as a response to dry conditions as it effectively reduces the leaf area over which transpiration can take place.

This is exhibited by plants of *F. ixioides* and *F. arenicola* var. *erecta*. In *F. ixioides* subsp. whereas distributed in the wetter south-western Cape the leaf blades are lax and broad and flattened, whereas in subsp. *glabra* distributed in the drier north-western Cape, the blades are rigid, subcylindrical and stem-like.

In many species the leaf blades exhibit a considerable range of form. Nevertheless, if used judiciously, this character is useful as an easily observable means of distinguishing those taxa in which blade form is reasonably constant and distinct. This applies especially to taxa with blades that represent extremes in the range of form.

Anatomical studies of leaf blades by Arnold (unpublished) suggest that internal structure will provide more valuable diagnostic features on which to distinguish taxa and on which to base relationships, than the gross morphology of the leaves.

Inflorescences

Inflorescences in the majority of species within the section *Bracteosae* are characteristically compact and are surrounded by an involucre of bracts. The bases of these bracts are conspicuously dilated and envelope the lower third or more of an inflorescence. The apices of the lowest 2–7 of these bracts are conspicuously attenuate into linear, photosynthetic blades that closely resemble leaf laminae.

Despite this superficial uniformity in external appearance, considerable variation is found on dissection of the inflorescence. The structural differences found, appear to be the result of different degrees of reduction within the inflorescence.

An explanation of inflorescence structure within the section *Bracteosae* is given as an aid to understanding the process of reduction that is evident.

In its most complex form the inflorescence comprises a central axis (axis 1, Fig. 3A*) that bears up to 12 or more, spirally imbricate bracts (b). These bracts are alike structurally but decrease progressively in size from base to apex. Developed in the axil of each bract is a partial inflorescence, the size and complexity of which also decrease progressively towards the axis apex.

Each partial inflorescence comprises an axis of the second order, axis 2. At the base of this axis two distichous appendages (p), are situated, one slightly

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* The diagrams in (Fig. 3) are schematic representations of steps in the sequence of reduction represented within inflorescences of taxa of the section *Bracteosae*. They have been simplified for ease of drawing. No attempt has been made in this study to undertake accurate comparative morphological interpretation of the different structures represented within the inflorescences, as it was felt this was a study in itself. For taxonomic identification comparisons between structural types are considered sufficient.

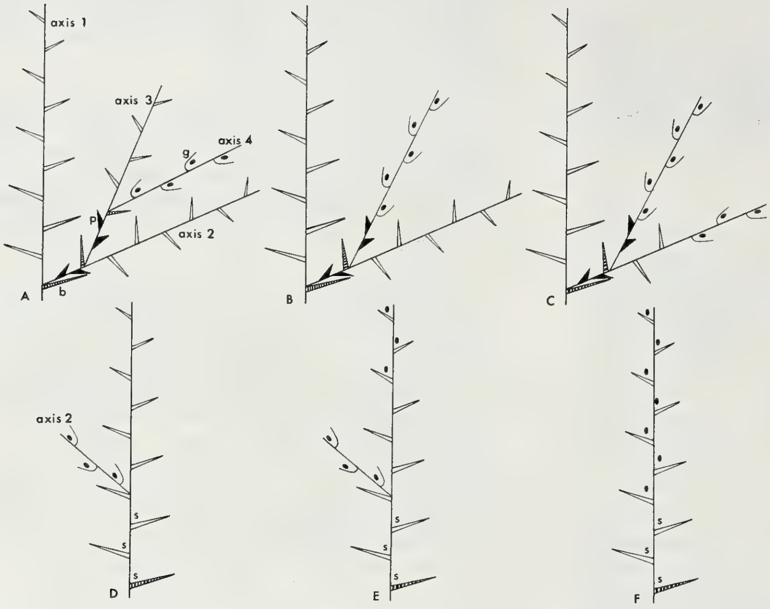

FIG. 3.—Inflorescence forms: diagnostic representation of the reduction series in *Ficinia* section *Bracteosae*. A, most complex form; B–E, intermediate forms; F, most reduced form; b, bract subtending partial inflorescence or floret (partial inflorescence comprising axes 2–4); p, prophyll; g, glume; s, empty bract.

above the other. These differ in form from the bracts and are empty. They represent prophylls and will be referred to as such in the remainder of the text. Above the prophylls a number of spirally imbricate bracts are situated, also designated (b), since they resemble in structure the bracts on axis 1 and, like them, decrease in size towards the axis apex.

Each of the bracts along axis 2 subtend an axis of the third order, axis 3. Two distichous prophylls (p) similar in structure to those on axis 2 are situated at the base of this axis. Above these prophylls are a number of spirally imbricate bracts (b) resembling again the bracts on the first and second order axes.

The bracts on axis 3 each subtend an axis of the fourth order, axis 4. This axis carries a number of fertile bracts which, since each subtends a single bisexual flower and differs in form from the bracts (b), are considered to represent glumes (g). Axis 4 therefore represents what, in species within *Scirpeae* (which presumably have undergone much reduction) is usually interpreted as a spikelet. This form of inflorescence was found in *F. pallens* and *F. arenicola.*

In the remaining species varying degrees of reduction of this inflorescence form are represented. The principal effect of reduction is to decrease the number of axes comprising each partial inflorescence (see Fig. 2B & C); to decrease the number of partial inflorescences per main axis (see Fig. 2D) and to reduce the number of prophylls or to eliminate these (see Fig. 3D–F, in which prophylls are entirely lacking.)

With the loss of a single axis within the partial inflorescence, axis 4, a condition represented in (Fig. 3B) resulted. Here, each of the bracts on axis 3 subtends a single bisexual flower. These bracts have the form and function of glumes, (they resemble the glumes on axis 4 in Fig. 3A and therefore are designated — g).

In most taxa, reduction of the partial inflorescence is not uniform, being more pronounced at the apex of the different taxa than at their bases. This results in the condition (Fig. 3C) in which the upper bracts of axis 2 each subtend a single bisexual flower, while the lower bracts subtend a complete axis, axis 3. This state is found in *F. elatior* and *F. ixioides.*

In some species the partial inflorescence is reduced to a single axis, axis 2 (Fig. 3D). The bracts on this axis resemble glumes and each subtends a single bisexual flower. In such taxa it is common for bracts on the upper portion of axis 1 to subtend single bisexual florets, while bracts on the lower portion of the same axis subtend a complete axis, axis 2 (see Fig. 3E). Characteristic of this inflorescence form are the empty 2–8 lowest bracts on axis 1, which have lost their axillary partial inflorescences.

The ultimate stage in reduction is an inflorescence comprising a single axis, axis 1 (Fig. 3F). The lowest 2–10 bracts on this axis are always empty, the remaining bracts each subtend a single bisexual flower. In this unispicate inflorescence form and the type shown in Fig. 3D & E, the bracts that subtend single bisexual flowers have maintained their bracteaceous nature, this is, however, not the case with the bracts of axis 2 and 3 of Fig. 3A–C, which also subtend single flowers but which are glumaceous, being thinner, softer, smaller, more membranous and pallid and less obviously longitudinally striate.

Accompanying the reduction of the branching axes is a reduction in the number of prophylls (p) at the base of each axis of the partial inflorescence. The inflorescence forms exhibited in Fig. 3A–C, all have a pair of distichous prophylls at the base of axes 2, 3 and 4?. In the inflorescences of *F. compasbergensis* Drège, *F. fascicularis* Nees, *F. monticola* Kunth, *F. pinguior* C.B.Cl. and *F. anceps* Nees, also included in the section *Bracteosae* by Pfeiffer (1920), only a single prophyll is situated adaxially at the base of each of these axes. Apart from exhibiting a single prophyll the first three taxa above also have branching inflorescences, considered to be a typical of the section *Bracteosae* in which the majority of taxa have, compact capitate inflorescences enveloped to a lesser or greater degree by an involucre of dilated inflorescence bracts. These three taxa are therefore, on the grounds of inflorescence form, tentatively excluded from the section *Bracteosae* pending revision of all the sections in the genus.

Although the single prophyll conditions suggests a more reduced condition from paired prophylls, this may not be the case in *Ficinia*. In this genus the progression in prophyll number is considered to have been from 1→2→0. This sequence is suggested firstly by the fact that taxa with a single prophyll include those with branching inflorescences, generally regarded as representing a condition of limited reduction in the Cyperaceae. Secondly those taxa exhibiting the most inflorescence reduction are all wanting in prophylls. In all these taxa, except one, *F. nigrescens* (Schrad.) J. Rayn., reduction of the branching system is complete, producing a unispicate inflorescence. In *F. nigrescens* reduction is not always maximal so that, together with plant bearing unispicate inflorescences, there are also plants in which all or few of the lateral branching systems (partial inflorescences) constitute single spikelets. In both these conditions prophylls were found to be wanting.

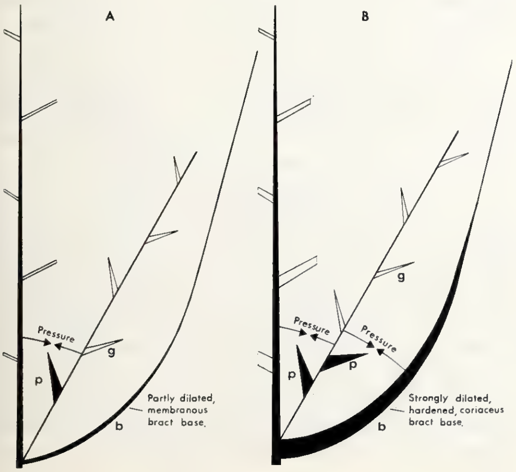
A
B
Pressure
Pressure
Pressure
p
p
p
g
g
b
b
Partly dilated, membranous bract base.
Strongly dilated, hardened, coriaceus bract base.

FIG. 4.—Prophyll states: A, single prophyll state characteristic of all sections other than section *Bracteosae;* B, double prophyll state represented by the majority of taxa in the section *Bracteosae.*

The three prophyll states in *Ficinia* are considered to be related to the degree of reduction in number and size of branching axes comprising each partial inflorescence. With compaction there is a comparable increase in pressure on the internal structure of the inflorescence, this being greatest in the axil of each branch in the region of the lowest adaxially situated bract (Fig. 4A). The result being to alter its size and structure transforming it into what is commonly referred to as a prophyll. This situation represented by the single prophyll condition is found in the majority of taxa in *Ficinia.*

In the section *Bracteosae,* compaction of the inflorescence has been accompanied by a change in the nature of the inflorescence bracts. The base of each bract has to a lesser or greater degree become dilated, expanding around the partial inflorescences in the form of an involucre. The dilated portions have also become thickened, hard and rigid. The result has been to further increase the internal pressure within the inflorescence, this time concentrated in the region of the second lowermost bract of each axis (Fig. 4B), reducing it to a further prophyll.

The degree of dilation, thickening and hardening of the inflorescence bracts decreases progressively towards the centre (apex) of the inflorescence. Because of this the extent to which the two lowermost bracts/glumes on axes 3 and 4 (Fig. 3 A–D) have been modified is generally less than in axes 1 and 2, so that they are not always distinguishable as prophylls. At the other extreme, the 1–2 lowermost bracts of axis 1 exhibiting the greatest degree of dilation and hardening, and therefore the greatest pressure, are in many taxa sterile.

In those taxa, in which prophylls were wanting, the number of sterile bracts at the base of axis 1 ranged between 2 and 6. This increase over taxa with 1–2 sterile bracts (plants with double prophylls) is probably due to the overall increase in dilation and hardening of bracts along axis 1. In these taxa the increased pressure along axis 1 has not only caused the loss of the double prophyll condition but has also reduced each partial inflorescence to a single floret. Therefore, whereas in most Cyperaceae the absence of prophylls represents a less specialized condition of limited reduction, in the section *Bracteosae* of *Ficinia* this condition is synonymous with maximum reduction and specialization.

In *F. pinguior* C.B.Cl., placed by Pfeiffer in the section *Bracteosae* although the inflorescence bracts have undergone dilation they have not become thickened or hardened. As this taxon exhibits a single prophyll condition, hardening of the bracts is seen as an essential factor responsible for the production of the second prophyll. Another taxon in which this may be observed is *F. paradoxa* (Schrad.) Nees, placed by Pfeiffer in the subsection *Capitulae* of the section *Isolepiformes*. *F. pinguior* is considered here to be more closely related to this taxon than any of the taxa included in the section *Bracteosae*. It is not known at this stage whether *F.*

pinguior with *F. paradoxa* should be included within the section *Bracteosae* or not. The evidence so far gathered suggests not, and *F. pinguior* is therefore tentatively excluded from the section pending revision of the genus.

Also included by Pfeiffer in the subsection *Capitulae* of the section *Isolepiformes* are *F. argyropa* Nees (=*F. paradoxa* (Schrad.) Nees var. *argyropa* (Nees) C.B.Cl. and *F. laevis* Nees. Not only do these two taxa have hardened, dilated bases to the inflorescence bracts, but they also exhibit the double prophyll condition. Their closest ally within the genus is considered to be *F. indica* (Lam.) Pfeiff. On the basis of this they are included here in the section *Bracteosae.*

Another species warranting special consideration is *F. ancepts* Nees, also considered by Pfeiffer to belong to the section *Bracteosae.* This taxon has only a single prophyll per inflorescence axis. Although its bracts have undergone dilation and hardening this is not so marked as in other taxa in the section. The lowest bract and partial inflorescence in many plants is up to 1,5 cm distant below the partly compacted upper section of the inflorescence. It therefore probably represents an intermediate stage towards the development of section *Bracteosae. F. anceps* is most closely allied to *F. fastigiata* Nees. This latter species also exhibits a single prophyll condition and is included by Pfeiffer in subsection *Capitulae* of the section *Isolepiformes. F. anceps* has therefore also been omitted from this treatment of the section *Bracteosae* until its relationship with the rest of the genus is better understood.

It should perhaps be noted at this point that prophylls are associated only with the axes that comprise partial inflorescences. It is probable that these appendages, despite their different appearance, are morphologically equivalent to the bracts of ancestral less reduced inflorescences. This has been accepted by Blaser (1944) and Koyama (1961) but, perhaps, needs further confirmation from anatomical and vascular investigation. The recording of the presence of prophylls in inflorescences within the section *Bracteosae* is an important step forward in appreciating the heterogeneity of *Ficinia* as it is at present delimited. Prophylls have not been recorded previously for the genus and they are certainly absent from those of its species with ‘simpler’ more reduced spikelets that are of the *Scirpus* type.

The degree of reduction of the inflorescence is not completely constant within each species. Many taxa exhibit two or occasionally three (for example *F. nigrescens)* inflorescence forms. Despite this the degree of reduction of the inflorescence, together with the number of prophylls present, are extremely important characters by which to distinguish different taxa within this section.

Style and style branches

Three main types of style are represented in the taxa studied. The differences between these types depend mainly upon robustness, slenderness and on relative lengths of style and style branches. In the commonest type, the style and its branches are slender and relatively elongate, pale brown and flecked with darker markings, with the style branches obviously papillate. The lengths of the fused lower portion of the styles relative to those of their branches varied considerably within the section and proved to be a useful means by which to distinguish many species. In some taxa the fused section is short (1–2) mm in length with very long branches 6–10 times the length of the fused section, for example *F. capitella* and *F. arenicola* var. *arenicola* (Fig. 2a). In other taxa the fused section and branches are approximately equal in length, for example *F. ixioides* (Fig. 2b).

The second type comprises styles that are notably broad and stout, red or pale brown with brown flecks and with the style branches granular rather than obviously papillate. The difference in appearance of the style branches depends upon the reduced length of the papillae. Examples of this type are *F. cedarbergensis* and *F. levynsiae* (Fig. 2c).

The styles of *F. radiata,* which also belongs to the second type (Fig. 2d), are characteristic of this species alone. They are broad, stout and granular and either lacked branches entirely or possessed three minutes notches at the style apex that represented branches. On these features, together with a few other individual characters, this taxon was at one time placed in *Sickmannia,* a monotype genus distinct from *Ficinia.* (Such a treatment is not upheld by Arnold, 1979.)

Anthers

Anthers in *Ficinia* are crested. In the section *Bracteosae* the shape and degree of development of the crests provided a useful additional character by which to delineate many of the taxa.

Five basic forms are recognized (Fig. 2j–o). These fall into two broad groups. The first group includes those with crests as long as, or shorter than, their breadth at the base of the crests, group two includes taxa with crests twice, or more than twice, as long as their breadth at the base of the crest.

In the first group the crests are either flattened or slightly rounded, globular or triangular (Fig. 2j–l). In the second group the crests are either linear-oblong with rounded apices (Fig. 2m) or linear-accuminate with pointed apices (Fig. 2n).

These five forms are not altogether clearly defined and some intermediates, did exist within species, nevertheless the shape of anther crests does provide an ancillary character useful in taxonomic diagnosis. The presence or absence of spines on the crests is also useful taxonomically. In *F. ixioides* subsp. *ixioides* (Fig. 2o) the crests bear long conspicuous spines (stiff and possibly silica-containing) while in subsp. *glabra* (Fig. 2n) these are minute (virtually absent). This is, therefore, a useful character in distinguishing between these infraspecies.

Achenes

Achenes of the different taxa differed in size, shape, colour and surface texture.

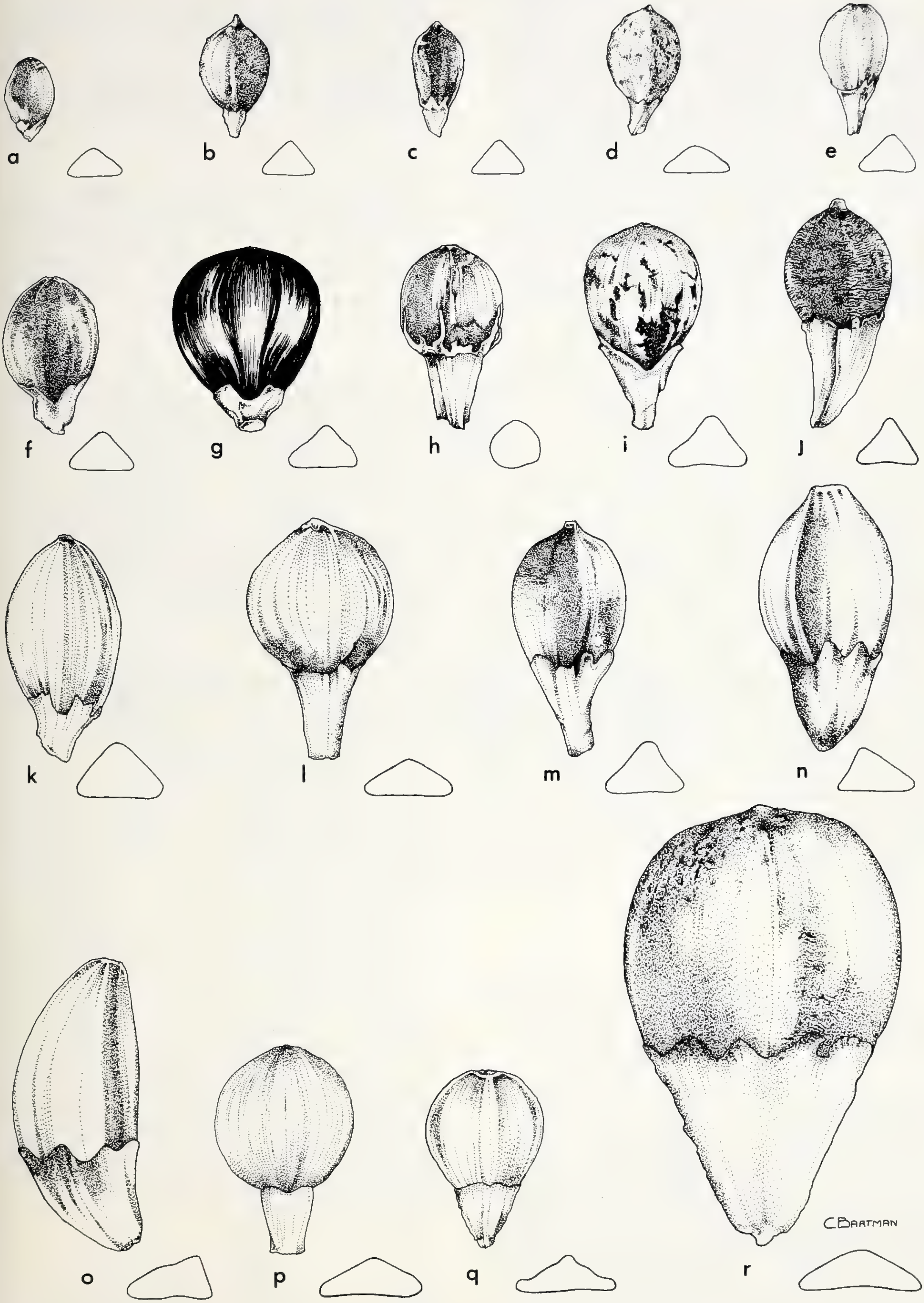

FIG. 5.—Achenes and gynophores; a, *F. pusilla;* b, *F. indica* taxon *indica;* c, *F. capitella;* d, *F. arenicoal* var. *erecta;* e, *F. pygmaea;* f, *F. nigrescens;* g, *F. ixioides* subsp. *glabra;* h, *F. latifolia;* i, *F. arenicola* var. *arenila;* j. *F. dunensis;* k, *F. pallens* var. *lithosperma;* l, *F. petrophylla;* m, *F. pallens* var. *pallens;* n, *F. cedarbergensis;* o, *F. levynsiae;* p, *F. gydomontana;* q, *F. grandiflora;* r, *F. deusta* (all × 10). Insets represent shape, in transverse section, at widest part (not drawn to scale).

Achene size ranged from 1,5–2 mm in length by 1 mm wide *(F. pusilla* Fig. 5a) to ± 6 mm in length by ± 4 mm in width (*F. deusta,* Fig. 5r). On individual plants and within taxa there is generally little size variation despite the fact that, especially in herbarium material, it is sometimes difficult to establish whether the achenes are fully mature and fertile or not. Achenes are usually three-angled or trigonous but often the ridges are not very sharp; mostly the faces equal each other in width (*F. ixioides* Fig. 5g), but in *F. cedarbergensis* (Fig. 5n) and *F. levynsiae* (Fig. 5p) they are unequal resulting in asymmetrical achenes. In *F. deusta* (Fig. 5r) and *F. grandiflora* (Fig. 5q) achenes are planoconvex, whereas in *F. latifolia* they are spherical (Fig. 5h).Achene apices also differ in some taxa. Most apices are obtuse or rounded; a few are acute often with a distinct but small beak for example *F. capitella* (Fig. 5c) and *F. dunensis* (Fig. 5j), whereas others are broad and flattened or retuse as in *F. cedarbergensis* and *F. levynsiae* (Fig. 5n & o).

The surface texture of the achenes is smooth and often polished, for example *F. ixioides* subsp. *glabra* (Fig. 5g), finely dotted (muricate), for example *F. indica* taxon *indica* (Fig. 5b), or transversely ridged as in *F. capitella* (Fig. 5c) and *F. dunensis* (Fig. 5j). Surface patterning of the achenes differs only negligibly within taxa therefore achene size, shape and surface markings are useful criteria in identifying taxa. Achene colour is not so satisfactory. All immature nuts are more or less uniformly pale yellow to brown in colour. This colour changes with maturity to black, grey, brown or red. Although there is a difference in achene colour between species at maturity, the possibility always exists that there is a colour range as the achenes develop to full size on the plant after fertilization so that no one colour is specific for a taxon. There is also no guarantee that unfertilized achenes follow the same colour sequence during development nor that achene colour does not alter in the herbarium. Consequently not much reliance should be placed on this character in taxonomic diagnosis.

Gynophore

The presence of a gynophore below the achene was (and still is) generally accepted as the main character that distinguishes *Ficinia* from its allied genera. Despite this, there have been included within *Ficinia* several taxa that lack a gynophore.

As mentioned earlier Clarke (1898) felt that it was difficult to attach much importance to the gynophore in *Ficinia.* Although this may certainly be true in the diagnosis of generic limits it does not apply infragenerically. The present investigation has shown there to be little variation in gynophore form within species and subspecies but from one taxon to another gynophore shape and degree of specialization of the margins differed markedly thus being a satisfactory character on which to recognize many species and sometimes infraspecific sub-units.

In the section *Bracteosae* the gynophore envelopes the lower portion of the achene. It shows a considerable range in variation from two or three lobed as in *F. nigrescens* (Fig. 5f), to cup-shaped with the upper margin crenate as in *F. levynsiae* (Fig. 5o) or developed into prominent finger-like projections as in *F. latifolia* (Fig. 5h).

The length of the gynophore relative to the total length of the achene is also a useful character. It ranges from 1/6 to 2/3 of the total achene length.

Inflorescence axis

After the bracts glumes and achenes have fallen, the inflorescence axis persists at the apex of the culm, remaining intact until the culm breaks up. Since the old culms often persist until after the following flowering season the form of the inflorescence axis is a readily available character with which to distinguish many taxa in the section *Bracteosae.*

The least reduced inflorescence axis shows a structure in which the branches associated with bract scars occur at intervals through the axis (Fig. 6a). More reduced types have branches restricted to the upper third of the axis with bract scars below (Fig. 6h). Inflorescences where the greatest reduction had taken place resulted in unbranched axes that resemble elongate empty strobili (Fig. 6n & p). Some breakage of these axes especially falling of the small branchlets probably takes place as they age and become weathered but, apart from these changes (which may be slightly misleading), persistent axes provide a convenient and reliable character for identifying taxa.

The sequence of reduction exhibited in the inflorescence is reflected in the structure of the inflorescence axis. A number of possible lines of reduction are apparent. In the first (Fig. 6a–e) reduction is concentrated within the main axis which becomes progressively shortened until in *F. capitella* it is almost receptacle-like. Associated with this is an obvious loss in the number of branches originating from the main axis. A second possible line of reduction is indicated by Fig. 6f–j. Here the main axis has become swollen with a progressive loss in the number of primary branches, from the base of the axis upwards until in *F. petraphylla* all the branches are lost. Finally in Fig. 6k–p, the tendency has been for the main axis to become elongate with a total loss of branches in these taxa, except in *F. nigrescens* in which some members still retain their primary branches (Fig. 6m). In *F. ixioides* although the branches have been lost some individuals possess a single branch originating from the base of the main axis (Fig. 6k). This branch is often as well developed as the main axis, equalling it in length and giving the inflorescence axis a forked appearance (Fig. 6l). This branch if present is however generally smaller than the main axis.

CONCLUSION

Most previous workers tended to rely mainly on easily observed morphological features such as the presence or absence of leaf blades the nature of the leaf sheath together with the presence or absence of a ligule, and the gross structural form of the inflorescence. Only when these characters failed was there any searching for less obvious differences such as the structural features of glumes, style and achene. Consequently, many highly suitable characters that could have been used to define the different taxa clearly and which would have provided a better understanding of the interrelationships within the genus, were not considered.

This investigation has revealed a number of characters within the inflorescence previously unused in classification. These include: the structure of the inflorescence, the presence, absence and number of prophylls, the style and style-branches, anther crests, achenes, gynophores and inflorescence axis. These have provided a valuable means by which the limits of many existing taxa have been refined. They have also provided the basis on which a number of new taxa have been established (Arnold & Gordon-Gray, 1978). Therefore their use has clarified, or partially clarified, some of the taxonomic confusion that existed within the genus, and by this has improved understanding of relationships within it.

UITTREKSEL

Die grense van die genus Ficinia *word hersien. Morfologiese variasie binne die afdeling* Bracteosae

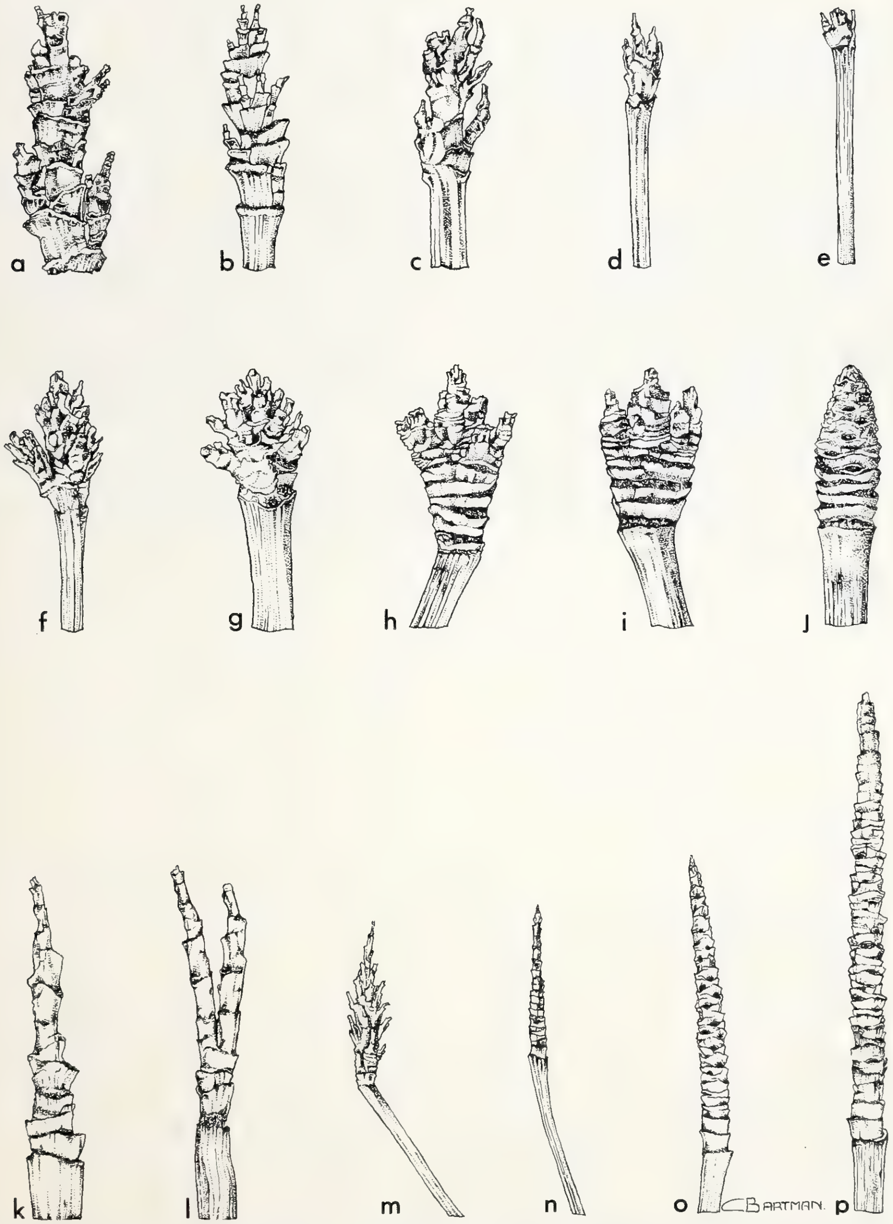

FIG. 6.—Inflorescence axes after floral parts have fallen: a, *F. pallens;* b, *F. latifolia;* c, *F. indica;* d, *F. capitella;* e, *F. dunensis;* f, *F. elatior;* g, *F. radiata;* h, *F. cedarbergensis;* i, *F. levynsiae;* j, *F. petrophylla;* k & l, *F. ixioides;* m, *F. nigrescens;* n, *F. nigrescens* and *F. gydomontana;* o, *F. grandiflora;* p, *F. deusta.* (*all* × 3).

Pfeiff van Ficinia *Schrad. (Cyperaceae) word bestudeer en bespreek. Kenmerkende eienskappe wat voorheen in klassifikasies gebruik is, word saam met 'n aantal nuwe eienskappe hersien. Hulle het dit moontlik gemaak dat die grense van baie bestaande taksa duideliker vasgestel kan word en het die grondslag verskaf waarop 'n aantal nuwe taksa wat onlangs beskryf is, vasgestel kon word. Eienskappe wat bestudeer is, sluit in: ondergrondse organe, blaarskedes, ligule, blaarskywe, strukture van bloeiwyses, skutblaartjies, style, helmknoppe, dogvrugte, stamperstele en die asse van bloeiwyses.*

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The genus *Medicago* (Leguminosae) in southern Africa

C. H. STIRTON*

ABSTRACT

Four species of *Medicago* have become naturalized in southern Africa: *M. laciniata, M. polymorpha, M. sativa* and *M. lupulina.* Their morphological variation and geographical distribution is discussed and a key is provided.

The genus *Medicago* is probably known to most readers from an acquaintance with lucerne, *Medicago sativa* L. This crop is the modern day 'King of forages', especially so in southern Africa where it is widely cultivated.

Representatives of the genus have been widely dispersed around the globe during the last two hundred years and today occupy important niches either as crops or weeds. Their weediness has much to do with their predominantly self-breeding and annual habits, some 75% of all species being annuals. These two features have allowed the expression of widespread variation especially at the infraspecific level. This, combined with known instances of polyploidy, has been the cause of much taxonomic confusion.

Diploids, tetraploids and hexaploids have been shown to occur in *Medicago* (Lesins & Lesins, 1980). Most of the diploids are of the 2n = 16 type, with a basic chromosome number of x = 8. Four species of diploids have 2n = 14 chromosomes and one has members with 2n = 16 and 2n = 14. The importance of ploidy in the evolution of *Medicago* has been discussed by Lesins & Lesins (1980) in their taxogenetic investigation of the genus. As I have not investigated ploidy in the four naturalized species of *Medicago* treated in this survey, such an investigation will be necessary when the infra-specific categorization of the South African 'naturalants' is studied in the future. It will be important in such a study to be aware of the Australian experience (McComb, 1974) where it was found that some forms of Medics did not always show the same range of characteristics for the species as a whole, as in Heyn (1963). Such is the case in southern Africa. For example, in *M. laciniata* (L.) Mill. the var. *laciniata* is generally separated from var. *brachyacantha* Boiss. as follows (McComb, 1974):

- Burrs with 5–8 coils, olive-shaped or globular, peduncle longer than the petiole, stipules laciniate, at least some leaves laciniate .... var. *laciniata*
- Burrs with 3–4½ coils, cylindrical, peduncle shorter than petiole, stipules incised, leaves dentate .... *var. brachyacantha* Boiss.

This key breaks down in southern Africa. Specimens here range from markedly laciniate-leaved forms with peduncles shorter than the petioles to specimens with large many-coiled burrs and petioles longer than the petiole.

Rather than attempt a classical morphological analysis of the infraspecific categories, an unsatisfactory approach for such levels anyway, it was decided to defer such a study until the plants could be investigated cytologically and ecologically. However, as *M. polymorpha* L. var. *brevispina* is distinctive enough it is recognized accordingly.

Four species of *Medicago* have become naturalized successfully in southern Africa: *M. sativa* L., *M. lupulina* L., *M. laciniata* (L.) Mill. and *M. polymorpha* L. Other species have also been grown in South Africa but have not persisted in the wild. These include *M. arabica* (L.) Hudson, *M. arborea* L., *M. falcata* L., *M. intertexta* (L.) Mill., *M. orbicularis* (L.) Bartalini, *M. scutellata* (L.) Mill and *M. turbinata* (L.) All.

The three keys provided below appertain to the four naturalized species and are based on vegetative, floral and fruit characters respectively.

1. KEY TO SPECIES BASED ON MATURE BURRS

- Burrs smooth or with small tubercles:
  - Burrs single-seeded, black, with only the distant end coiled .... *M. lupulina*
  - Burrs many-seeded, brown, coiled along the full length:
    - Burrs smooth, veins emerging obliquely from the ventral suture, branching somewhat, then anastomosing in the outer part of the coil face .... *M. sativa*
    - Burrs tubercled, with 6–10 prominent curved veins anastomosing freely before joining the lateral vein .... *M. polymorpha* var. *brevispina*
- Burrs spiny:
  - Burrs with partitions between the seeds .... *M. polymorpha*
  - Burrs without partitions between the seeds .... *M. laciniata*

2. KEY TO SPECIES BASED ON FLOWERING PLANTS WITHOUT MATURE BURRS

- Corolla purple, mauve or pale lilac .... *M. sativa*
- Corolla yellow or golden:
  - Flowers 10–30, peduncle > 2× the petiole of the subtending leaf .... *M. lupulina*
  - Flowers 1–10, peduncle < 2× the petiole of the subtending leaf:
    - Calyx teeth longer than the tube, wing petals longer than keel .... *M. polymorpha*
    - Calyx teeth shorter than the tube, wing petals shorter than the keel .... *M. laciniata*

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3. KEY TO SPECIES BASED ON VEGETATIVE PARTS

Stipules deeply incised or laciniate:
  Central leaflets 4–6 mm wide, lower side of stipules covered in simple hairs .... *M. laciniata*
  Central leaflets 7–15 mm wide, lower side of stipules glabrous or with a few hairs along the margin .... *M. polymorpha*
Stipules entire or irregularly toothed:
  Margin of leaf slightly toothed in upper part .... *M. lupulina*
  Margin of leaf serrate in upper part .... *M. sativa*

1. **Medicago laciniata** (*L.*) *Mill.*, Gard. Dict. edn 8, *Medicago* no. 5 (1768); All., Fl. Pedem. 1: 315 (1785); E. Mey., Comm. 1: 92 (1836); Eckl. & Zeyh., Enum. 1504 (1836); Harv. in F.C. 2: 163 (1862); Heyn, Annual Sp. *Medicago:* 55 (1963); Schreib F.S.W.A. 60: 86 (1970); J. B. Gillett in F.T.E.A., Leguminosae 4,2: 1037 (1971); Jacot Guill., Fl. Lesotho: 192 (1971). Iconotype: plate 34 in Breyne, Exoticarum aliarumque minus cognitarum plantarum (1678), fide Heyn, l.c.

M. polymorpha L. var. *laciniata* L., Sp. Pl. 781 (1753).
M. aschersoniana Urb. in Verh. bot. Ver. Prov. Brandenb. 15: 77 (1873); Adamson & Salter, Fl. Cape Penins. 494 (1950)

Spreading annual up to 35 cm long, branching from near the base. *Vegetative parts* glabrous or sparsely pilose, especially on the petioles and lower surface of the leaflet-midribs. *Stipules* incised or laciniate, simple hairs on lower side only. *Petiole* up to 2 cm long; rhachis above lateral leaflets up to 5 mm long. *Central leaflets* 4–15 mm long, 2–7 mm wide, narrowly obovate or oblong, base cuneate, apex truncate, retuse and apiculate or tridentate, leaf margins serrate or irregularly laciniate, upper surface glabrous, lower surface sparsely pilose. *Racemes* 1–2 flowered, peduncle with a terminal cusp. *Florets* 4–6 mm long, pedicel shorter than the calyx tube; bract ± length of the pedicel. *Calyx* 2–4 mm long, sparsely covered with appressed hairs, teeth shorter than the tube. *Corolla* yellow, >2 × length of the calyx. *Standard* 4, 5–6, 0 mm long, ovate. *Wing petals* shorter than the keel. *Developing pod* glabrous, contracted but protruding sideways from the calyx, coiling anti-clockwise. *Mature fruits* 1(2) per raceme, olive-shaped, globular or cylindrical. *Coils* 5–7, turning clockwise, 3–5 mm in diameter, not strongly appressed, radial veins S-shaped, 8–16, and not anastomosing until they run into a protruding lateral vein, lateral veins adjoining the elevated dorsal suture as shoulders at right angles. *Spines* 8–16 in each row, 2–4 mm long, distinctly grooved in their basal part, inserted at 90°–180° to the coil face. *Seeds* 2–3 mm wide, 1, 0–1, 5 mm wide, 5–10 per pod, non-partitioned, oval—slightly reniform, pale yellow to yellow-brown; radicle up to $\frac{2}{3}$ seed length, tip clear but rarely curled out, hilum a small hollow. *Cotyledons* 10–16 mm long, 1,5–2,5 mm wide, narrowly cuneate-obovate. 2n = 16. Fig. 1.

Distribution

The natural habitat of cut-leaf medic is in dry, sandy or stony desertlike conditions. It is native to the southern coast of the Mediterranean Sea extending from the Canary Islands over North Africa to the drier areas of India and Pakistan (Lesins *et al.*, 1980). Elsewhere it is an adventitious weed. In southern Africa it has become naturalized in the drier hinterland and in a few isolated instances along the East Coast or nearby Agricultural Experimental Stations (Fig. 2). Like *Medicago* it is probably far more extensive in the Cape Province than existing herbarium material would indicate.

Common name

Sotho: Bohomenyana, the small 'Bohome'. Phillips (1917) says that this word is derived from ho

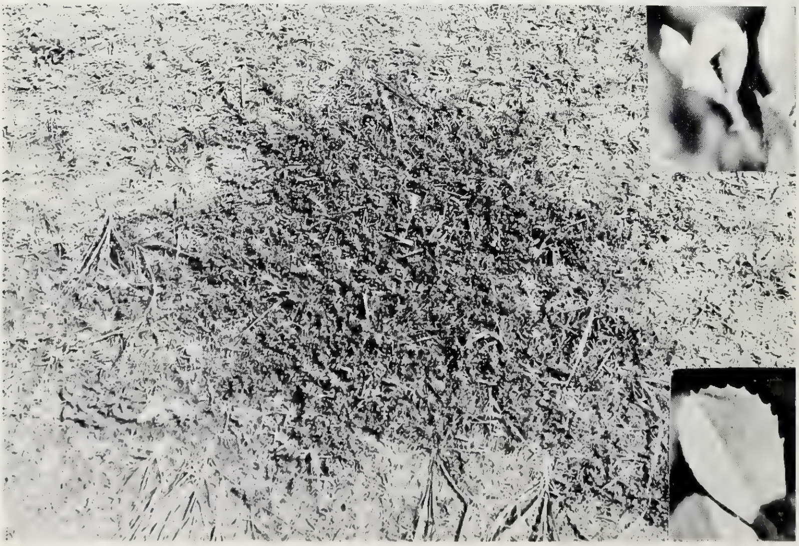


FIG. 1.—*Medicago laciniata.* Photo showing habit, leaf, and inflorescence of a plant growing near Port Edward, Natal.

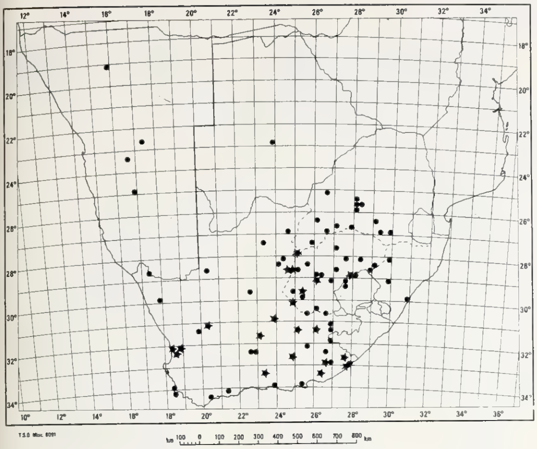


FIG. 2.—Known distribution of *Medicago laciniata* in southern Africa: ●, var. *laciniata;* ★, var. *brachyacantha.*

homa — to adhere or stick to, referring to the spiny fruits which adhere to clothing.

Ethnobotanical uses

According to Phillips (1917) cut-leaf medic is ground up finely and then as an infusion used as a love philtre.

Variation within species

Cut-leaf medic is a rather variable species. Infraspecific delimitation has been based in the past on the degree of laciniation of the leaflets and stipules, length of peduncles, size of pods, number, length, and angle of insertion of spines, and the number of veins on the coil face.

South African material has been commonly known as *M. aschersoniana* Urb., because of the widespread lack of laciniation in much of the South African material. However, experimental hybridizations (Lesins & Erac, 1968; Lilienfeld, 1959) have given successful crosses between *M. laciniata* and *M. aschersoniana,* so one must conclude that they are variants of a single species.

Although 10 varieties have been named in *M. laciniata* (Heyn, 1963) only two are generally recognized (Heyn, 1970, McComb, 1974): 1, var. *laciniata* with stipules and leaflets laciniate, peduncle longer than the petiole, pods with 5–7 coils and long spines; 2, var. *brachyacantha* Boiss. with stipules and leaflets serrate, peduncle equal or shorter than the petiole, pods with 2,5–4,5 coils and variable length of spines. These characters, as indicated in the introduction, break down in southern Africa. No purpose is served, therefore, in giving infraspecific categories for this material until a detailed field study is undertaken in South Africa (see for example Friedman & Orshan, 1974; Friedman & Elberse, 1976).

Distinction between species

Medicago laciniata is readily separable from *M. polymorpha* by its wing petals being shorter than the keel; the sigmoid, slightly branching, non-freely anastomosing radial veins on the pod face, seed radicle ⅔ the length of the seed and seeds not partitioned in the pod. More fundamentally *M. laciniata* is 2n = 16, whereas *M. polymorpha* is 2n = 14.

Vouchers

Acocks 7092, 7118, 9184, 9623, 16192, 16532, 18698; *Anderson* 243; *Archibald* 6147, *Badenhorst* 11,68; *Beeton* 108; *Bolus* 8984; *Bryant* 1134; *Brynard,* 110; *Burtt Davy* 9282, 10736, 10782; *Clarke* 512; *Class* 6; *De Victoria* 44; *Dieterlen* 147; *Du Toit* PRE 54930; *Ecklon & Zeyher* SAM 15386, 32123; *Flanagan* 1891; *Fourcade* 1567; *Galpin* 1651B; *Gerstner,* 92; *Gibbs Russell, Robinson, Herman & Downing,* 4254; *Giess* 3976; *Giess & Hübsch* 11603; *Giess, Volk & Bliessner* 6107; *Gill,* 28; *Goossens,* 651; *Grobbelaar* 658, 799; *Jacot Guillarmod* 417; *Hafström* 827, 1004; *Hanekom,* 924, 2121; *Henrici* 162, 2598; *Hughes* PRE 54968; *Jooste* 252, 313; *Junod* 17374; *Kinges* 1811; *Kretzschman* PRE 15694; *Landsdell* 1193; *Leendertz* 3762, 3985, 9443, 10923; *Leistner* 196, 829, 1507; *Marloth,* 793; *Marsh* 128; *Merxmuller & Giess* 28230; *Mogg* 11626, 15124, 16586, 16619, 16766, 16854; *Moran* 93, 1345A, PRE 19592; *Muller* 1837; *Obermeyer* 27806; *Orpen* 23; *Patterson* 513A; *Pohl* PRE 57978; *Pole Evans* 1624, 1741; *Pont* 379; *Potts* 2919, 2943, 3119; *Rattray* 1308; *Repton* 6925; *Roberts* 5442; *Rogers* 27478; *Schlechter* 1256, 4308, 5135, 10859, 12107; *Schmitz* 69, 227, 4215; *Silk, 57*; *Smith* 517, 1428, 3998, 4402; *Stephen Van Graan & Schwabe,* 961; *Stirton* 1056, 6082, 6223; *Story* 4923; *Strey* 7863; *Sutton* 262; *Taylor* 5263; *Theiler* 12027; *Theron* 57; *Thompson & Le Roux* 26; *Thorne* SAM 51905, 52517; *Van Breda* 540; *Van der Berg* 3922; *Van der Merwe* 1150; *Van Ginkel* 233; *Van Niekerk* 18978; *Ward* 5967; *Wasserfall* 1162; *Werdermann & Oberdieck* 1072AA; *Werger* 286; *West* 1127; *Whitlock* 549; *Wilman* 19593; *Wolff* 31; *Zeyher* 2370.

2. **Medicago lupulina** *L.*, Sp. Pl. 2: 779 (1753); Bak. in F.T.A. 2: 51 (1871); J. B. Gillett, in F.T.E.A., Leguminosae 4,2: 1013 (1971). Type: Europe, fide Heyn, in Bull. Res. Council Israel 7D: 162 (1959).

Short-lived perennial or annual herbs, prostrate to ascending, 20–60 cm long, branching from the base. *Vegetative* parts more or less densely covered with simple appressed hairs. *Stipules* entire or dentate, green, upper surface mostly glabrous, lower densely hairy, lanceolate. *Petiole* very short in upper leaves, up to 1,5 cm in lower leaves. *Central leaflets* from leaflets in rosette 4, 5–6, 0 mm long, 4, 5–7, 0 mm wide, orbicular–cuneate-obovate; leaves on branches 11–15 mm long, 6–11 mm broad, obovate–oval, pubescent on both sides, apex retuse or apiculate, margin slightly toothed in upper half. *Racemes* 5–25 flowered, exceeding the subtending petioles, elongating in fruit until 3–5 times the length of the petiole, slightly awned. *Florets* small, 2,5–3,5 mm long, pedicel shorter than the calyx tube, bract filiform. *Calyx* 1,0–2,0 mm long, pubescent, lateral and carinal teeth slightly longer and the vexillar teeth slightly shorter than the tube. *Corolla* yellow, about twice the length of the calyx. *Standard* 2–2,5 mm long, subrotund. *Wing petals* shorter than the keel. *Young fruit* contracted within the calyx, hairy. *Mature fruit* about 2,5 mm long, single-seeded, coiled distally, sparsely pubescent, black when ripe, veins numbering 3–6, curving obliquely from the centre, branching outwards but entering the dorsal suture without a change of direction. *Seed* 1,5–2,0 mm long, 1,0–1,75 mm wide, oval or round, yellow or yellow-brown; radicle longer than half the length of the seeds, tip distinct. 2n = 16,32: it is not known whether both cytotypes occur in southern Africa. Fig. 3.

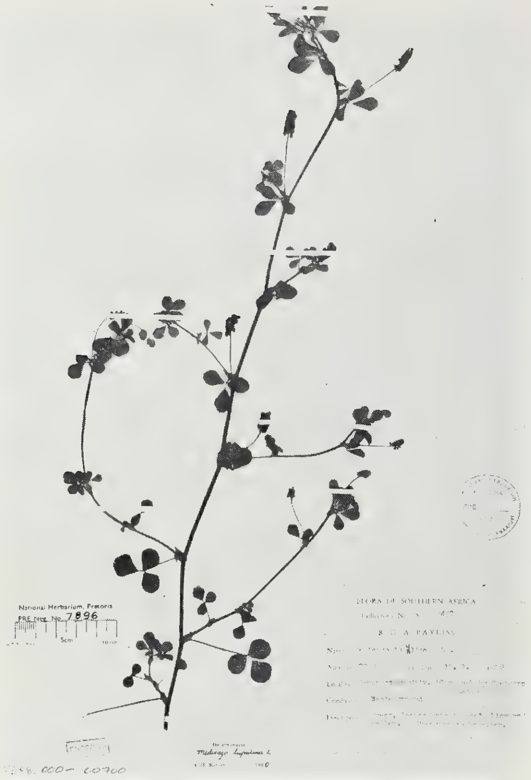


FIG. 3.—*Medicago lupulina (Bayliss* 8452).

Distribution

Black medic is a late-maturing species that has a preference for moister and cooler habitats than is the case for most annual medics. It occurs naturally in Europe, North Africa and most of Asia (Lesins & Lesins, 1980) and is an introduction in other temperate areas. In southern Africa it has been found occupying waste ground, hillsides, and is reported to be a weed of gardens, kikuyu *(Pennisetum clandestinum)* lawns and lucerne *(M. sativa* L.) fields (Fig. 4). It is apparently relished by livestock. In southern Africa it flowers predominantly in October, but extends well into January.

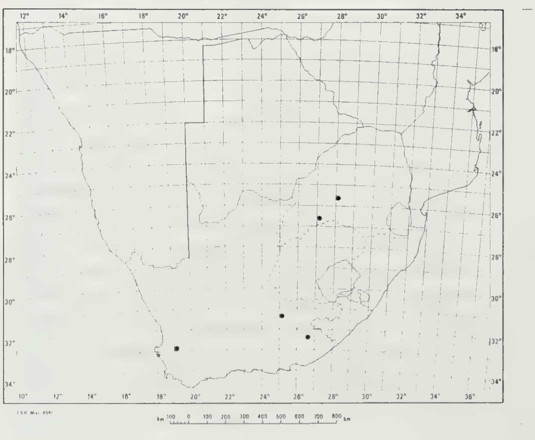


FIG. 4.—Known distribution of *Medicago lupulina* in southern Africa.

Variation within species

Black medic is fairly homogeneous in southern Africa and it is not expected that any striking variants will turn up in the future.

Distinction between species

Black medic is easily separated from the other three medics, naturalized in southern Africa, by its one-seed, non-dehiscent black fruits with their tips twisted into a small coil; and its large number of small flowers subtended by a peduncle that is equal to or greater than twice the length of the petiole of the subtending leaf. These features, together with the slightly toothed upper margins of the leaflets subtended by entire or irregularly toothed stipules, should be conclusive for a correct identification.

Vouchers

Acocks, 15952; *Bayliss* 8452; *Hanekom,* 1286; *Howlett,* 2622; *Louw,* 1080; *Obermeyer,* 27842; *Repton,* 1459; *Smith,* 1433; *Theron,* 527; *Ubbink,* 476. Cultivated: *Grobbelaar,* 174.

3. **Medicago polymorpha** *L.*, Sp. Pl. 2: 779 (1753), emend Shin. in Rhodora 58: 5 (1956); Heyn, Annual Sp. *Medicago:* 71 (1963); J. B. Gillett in F.T.E.A. Leguminosae 4,2: 1039 (1971). Type: Hort. Cliff., No. 118 (BM, lecto.)

M. nigra Krock., Fl. Siles. 2,2: 244 (1790); DC., Prodr. 2: 178 (1825); Eckl. & Zeyh., Enum. 1502 (1836); E. Mey., Comm. 92 (1836). Type: Unknown.

M. hispida Gaertn., De Fruct. 2: 349, t. 155 (1791); Adamson & Salter, Fl. Cape Penins. 494 (1950); M. D. Henderson & J. G. Anders., Common Weeds in S. Afr. 180 (1966). Type: fruit of unknown origin (?P, holo.).

M. denticulata Willd., Sp. Pl. 3: 1414 (1802); DC., Prodr. 2: 176 (1825); Eckl. & Zeyh., Enum. 1503 (1836); E. Mey. Comm. 92 (1836); Harv., in Harv. & Sond., Fl. Cap. 2: 162 (1862). Type: from S. Europe, Herb Willdenow no. 14327/4 (B. holo).

Annual procumbent herbs with many spreading branches arising at the crown of long tap roots and secondarily along the main branches. *Vegetative parts* glabrous except for a few hairs on the petiolules, lower surface of the leaflet-midribs, calyces and young peduncles. *Stems* up to 60 cm long, green, sharply angled. *Stipules* laciniate, green, ovate up to 10 mm long. *Petiole* up to 3–4 cm long. *Central leaflets* 9–20 mm long, 7–20 mm wide, cuneate to obovate, apex obtuse or retuse, apex apiculate, margin nearly entire or with 5–10 teeth each side of upper third. *Raceme* 1–5 flowered. *Florets* 4–6 mm long; pedical shorter than the calyx tube; bract longer than the pedicel. *Calyx* about 2,5 mm long; teeth more or less equal to the tube. *Corolla* yellow, 3–5 mm long. *Standard* broadly obovate, emarginate. *Wing petals* longer than the keel. *Developing fruit* initially contracted and protruding sideways from the calyx, coiling anticlockwise. *Mature fruits* 1–5 per raceme, discoid, short to long-cylindrical, or conical truncate, spiny tuberculate or spineless, mostly glabrous. *Coils* 1,5–7,0 not tightly appressed, 3,5–8,0 mm in diameter, turning clockwise; radial veins curved 6–15, anastomosing freely before entering the lateral vein, between it and the dorsal suture there is a prominent groove traversed by roots of spines and

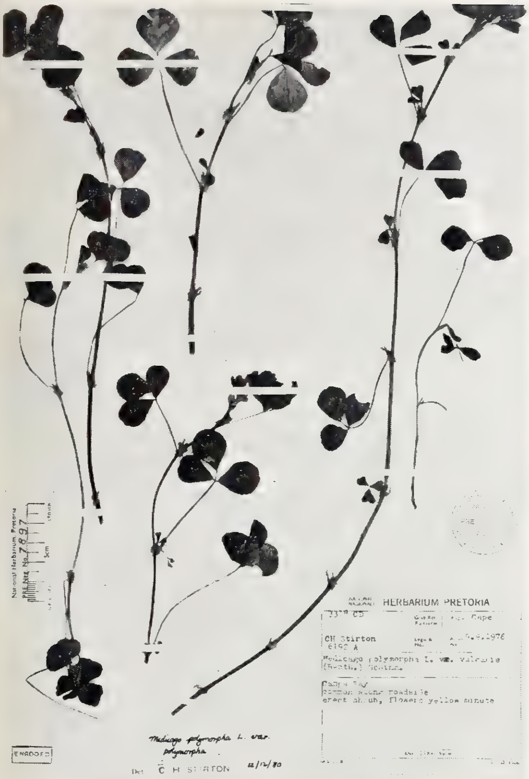


FIG. 5.—*Medicago polymorpha* var. *polymorpha (Stirton* 6192A)

tubercles. *Spines,* if present, up to 16 in each row, 0,5–4,0 mm long, grooved, inserted at 90° (on end coils) to 180° to the face of the coil, some hooked. *Seeds* 2,5–4,0 mm long, 1,5–2,0 mm wide, 4–8 per fruit, partitioned, oval to subreniform, yellow to yellow-brown; radicle equal to or less than half the length of the cotyledons, 2n = 14. Fig. 5.

Distribution

Burr medic is distributed through much of South Africa. This Mediterranean species has established itself in many parts of the world, where it has become a weed of cultivation and pastures. It is a nuisance in sheep farming areas as the burrs cling to wool thereby resulting in cheaper wool prices. In southern Africa it has been found along roadsides, in lawns and vegetable gardens, irrigation areas and in clover/kikuyu pastures (Fig. 6). Flowering occurs from August to December with a peak in September.

Common names

Klawergras (Afrikaans).

Variation within species

Like *M. laciniata,* burr medic is a rather variable species. [See Lesins & Lesins (1980) for a fuller discussion.] Infraspecific variants are usually distinguished on fruit characters. The three most common varieties are those accepted by Heyn (1963):

Pods spineless or tubercled (Fig. 9c) .... var. *brevispina* Heyn
Pods with spines:
    Diameter of coils 5–8 (10) mm, number of coils 4–6, spines thick and hardened, 1–5-flowered (Fig. 9a) .... var. *polymorpha*
    Diameter of coils 2,5–4,5 mm, number of coils 1,5–3,5, spines thin and slender, 5–10-flowered (Fig. 9b) .... var *vulgaris* Shin.

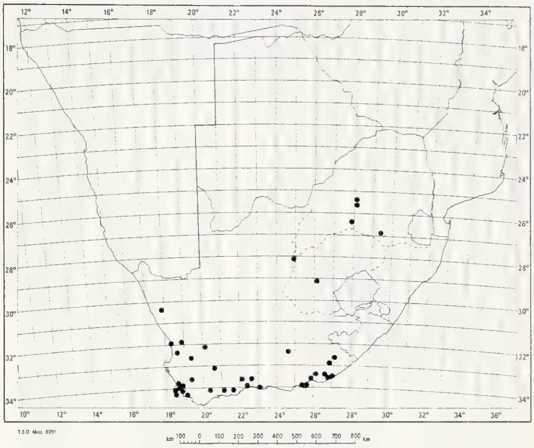


FIG. 6.—Known distribution of *Medicago polymorpha* in southern Africa.

Although there are plants in southern Africa which fit these categories there are others which do not; a similar finding to that of McComb (1974), who studied the naturalized medics in Western Australia.

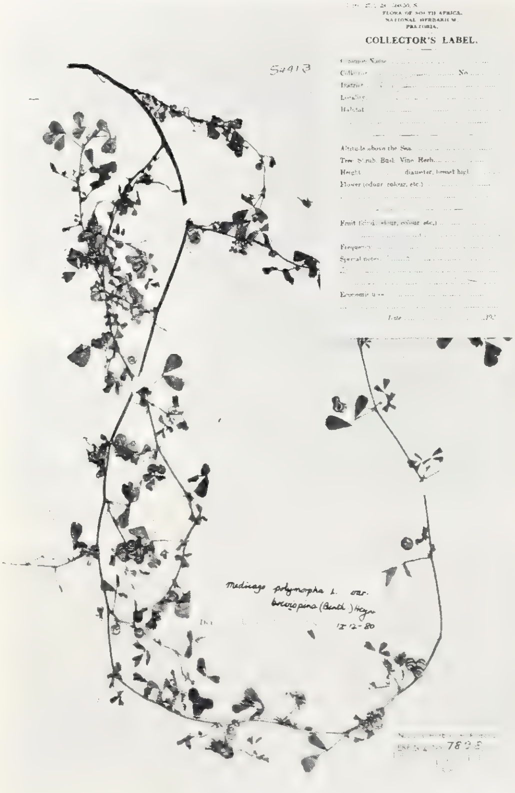


FIG. 7.—*Medicago polymorpha* var. *brevispina* (PRE 54913)

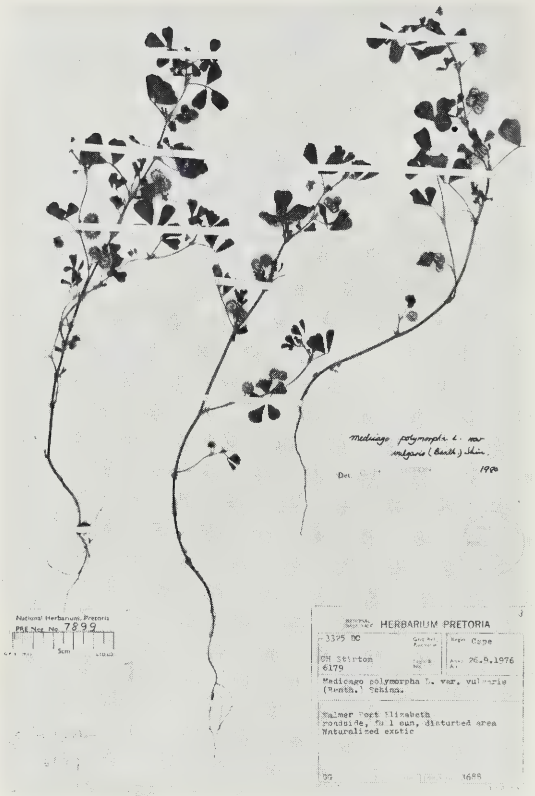

Medicago polymorpha L. var vulgaris (Benth.) Shin.
Det. 1980
National Herbarium, Pretoria
PRE Neg. No. 7899
5cm
HERBARIUM PRETORIA
3325 DC
Cape
CH Stirton
6179
26.9.1976
Medicago polymorpha L. var. vulgaris (Benth.) Schinn.
Walmer Port Elizabeth
roadside, full sun, disturbed area
Naturalized exotic
1688

FIG. 8.—*Medicago polymorpha* var. *vulgaris* (*Stirton* 6179)

As *M. polymorpha* is easily distinguishable from the other three medics in southern Africa, I will let the matter rest until an intensive experimental study is carried out on the infraspecific variation which occurs here.

Variation between species

The spiny forms of burr medic are often confused with cut-leaf medic, *M. laciniata*. A comparison of fruits easily distinguishes them, however. In burr medic there are thin partitions between the seeds, whereas in cut-leaf medic there are no partitions. Furthermore, the radial veins on the pod face are curved, never sigmoid, and anastomose freely. Another character that separates the two species is that in burr medic the wing petals are longer than the keel, whereas in cut-leaf medic the wing petals are shorter than the keel.

Vouchers

Acocks 9122; *Baker* PRE 54912, 54913; *Bloxam* PRE 10781, *Bolus* 79; *Brink* 184; *Britten* 12314; *Dahlstrand* 2350; *M. Drége* 3075, *Ecklon & Zeyher* 1502, 1503, 2370; *Foley* 95; *Gibbs Russell* 3401; *Gitten* 133; *Glass* 517; *Gordon* PRE 4624; *Grobbelaar* 274, 1388; *Hanekom* 2136; *Harvey* 7501; *Jenkins* 9946; *Jordan* s.n.; *Lansdell* 851; *Leendertz* 8363; *Marais* 439; *Marloth* 7198, 9428, 10831; *Mogg* 16855; *Muir* 1594, 2376; *Phillips* PRE 54998; *Potts* 2920; *Purcell*, 288; *Rogers* 16652, 27371; *Scott* PRE 54916; *Sim* 19440a; *Stirton* 5909, 5973, 5983, 6067, 6121, 6165, 6179, 6183, 6185A, 6192A, 6195A, 6226, 6377; *Story* 2779, *Taylor* 5275, 9888; *Van Dam* PRE 18850; *C. van der Merwe* 1300; *Wilman* PRE 54915, 54935.

4. **Medicago sativa** *L.*, Sp. Pl. 2: 778 (1753); Eckl. & Zeyh., Enum, 1501 (1836); E. Mey, Comm. 91 (1836); Harv., in Harv. & Sond., Fl. Cap. 2: 162 (1862); Adamson & Salter, Fl. Cape Penins. 494 (1950); Jacot Guill., Fl. Lesotho 82 (1971). For detailed discussions on synonymy see Iverson & Meijer (1967), Lesins & Lesins (1980), and Gunn, Skrdla & Spencer (1978).

Perennial herbs with 1 to many procumbent or ascending to erect stems up to 80 cm long arising from a stout crown and rootstock. *Vegetative* parts variously covered with simple appressed hairs. *Stipules* entire or basally toothed. *Leaflets* 10–25 mm long, 3–15 mm wide, obovate below becoming linear-oblanceolate higher up, serrate towards the apex, midrib ending in a terminal tooth. *Racemes* 10–35-flowered, elongate peduncle greatly exceeding the corresponding petiole, terminally awned. *Florets* 6–12 mm long, pedicel more or less equal to or longer than the calyx tube and the bract respectively. *Calyx* half the length of the floret, tube more or less equal to the teeth. *Corolla* purple, mauve or pale lilac. *Standard* oblong. *Wing petals* longer than the keel. *Young fruit* rises from the calyx, then bends sideways. *Mature fruits* 2,5–9,0 mm in diameter, spineless, coiled in a spiral, glabrous or with simple appressed hairs; coils 1–5, turning clockwise; many, starting from the ventral suture running obliquely, somewhat branching, then anastomosing in the outer part of the coil face. *Seeds*

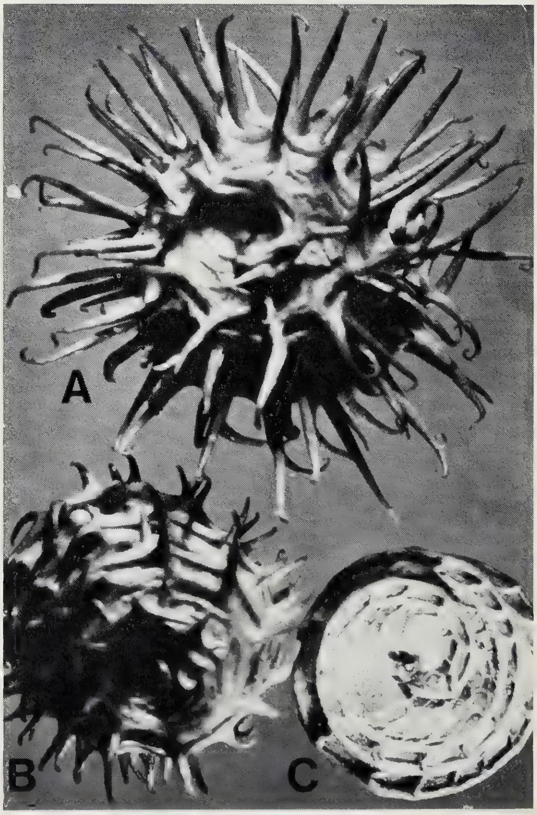


FIG. 9.—Fruits types in *Medicago polymorpha:* a, var. *polymorpha;* b, var. *vulgaris;* c, var. *brevispina.*

2–12, 1,0–2,5 mm long, 1,0–1,5 mm wide, yellow to brown; radicle just over half the length of the seed. 2n = 16,32. Fig. 10.

Distribution

M. sativa, lucerne or alfalfa, has escaped from cultivation in most areas where it has been cultivated in southern Africa (Fig. 10) It is particularly common along roadsides in some regions. Flowering occurs from October to February, but mainly during October and November.

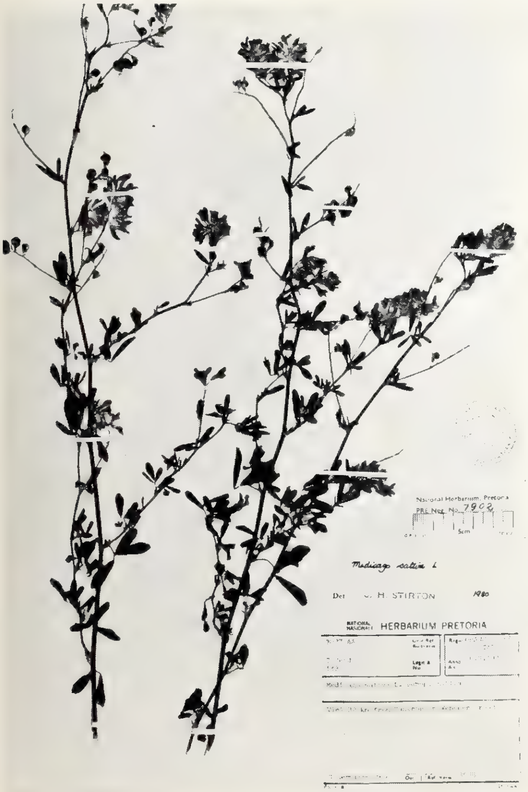
Jacot Guillarmod (1971) reports the occurrence of the rust *Uromyces striatus* Schroet. on plants cultivated at Mamathes in Lesotho.

Variation within species

Although some authors advocate nine subspecies in an expanded species description (Gunn, Skrdla & Spencer, 1978), others accept two subspecies in a narrower species description (Davis, 1970; Lesins & Lesins, 1980). The fragmentation of the *M. sativa* L. complex by Vassilczenko (1949), Sinskaya (1950) and others has been discussed by Lubenetz (1972), Lesins *et al.* (1980), and Iverson & Meijer (1967).

The two main subspecies recognized by most authors may be keyed out as follows:

Fruits 2–4 (5) mm in diameter, usually smaller than calyx; seeds 1,6–2,0 mm long; florets 5–6 mm long .... subsp. *coerulea* Schmalh.
Fruits 5–9 mm in diameter, concealing calyx; seeds 2,2– 2,5 mm long; florets 6–12 mm long.......... subsp. *sativa*


National Herbarium, Pretoria
PRE Neg. No. 7902
5cm
Medicago sativa L
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NATIONAL NASIONALE HERBARIUM PRETORIA

FIG. 10.—*Medicago sativa (Reid* 143)

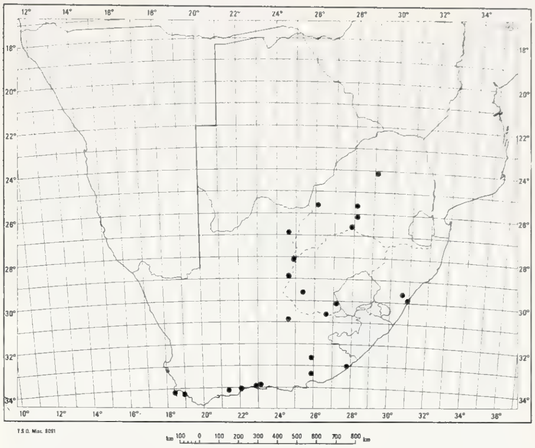

FIG. 11.—Known distribution of *Medicago sativa* in southern Africa.

Variation between species

M. sativa is easily recognized among naturalized medics by its purple, mauve or pale lilac flowers and its smooth, 2–12-seeded legumes.

Vouchers

Adams 108; *Alexander* PRE 54979; *Burtt Davy* 12610; *Ecklon & Zeyher* 1501; *Gerstner* 148; *Grobbelaar* 269, 438, 1231, 1304; *Johnson* 791; *Leendertz* 7378, 8364, 10914, 11132; *McClean* 800; *Moran* s.n.; *Muir* 1297; *Rattray,* 1278; *Reid* 143; *Scott* PRE 54983; *Stirton* 6171, 6331; *Theiler* PRE 54975; *Vahrmeijer* 2233; *Verdoorn* 953; *Victoria* 48; *Walker Moss Herb.* 26829; *Walters* PRE 8115; *Wells* 1445.

Cultivated medics

The following species have been cultivated in southern Africa at some time or other in the past. None have yet been collected from the wild as persistent escapes.

1. **M. arabica** (*L.*) *Huds.,* Fl. Angl. 288 (1762). *M. polymorpha* L. var. *arabica* L., Sp. Pl. 780 (1753).

Spotted burr medic is characterized by the purplish brown blotch (sometimes absent) on each leaflet and the coiled burr-like pod. It is similar to burr medic, *M. polymorpha,* but differs from that species in its multicellular hairs, distinctly toothed stipule margins and dorsal suture in a groove. A coil viewed from the edge has 3 grooves and 4 ridges. The radicle is longer than half the length of the cotyledons.

Voucher

Grobbelaar 1975.

2. **M. arborea** *L.,* Sp. Pl. 778 (1753).

Tree medic is a 1–4 m high perennial shrub densely covered in appressed silky hairs. It bears large yellow to golden flowers, has entire, triangular stipules and large spirally coiled smooth pods.

Vouchers

Codd 2484; *Grobbelaar* 1377; *Melle* (20/09/1919), *Theron* 44.

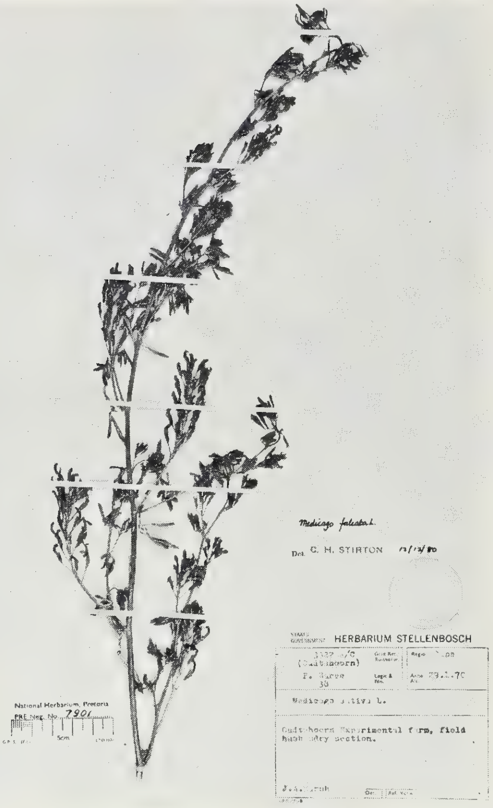

FIG. 12.—*Medicago falcata (Maree* 38)

3. **M. falcata** *L.*, Sp. Pl. 779 (1753). *M. sativa* L. var. *falcata* (L.) Döll, Rhein Fl. 802 (1853); *M. sativa* L. subsp. *falcata* (L.) Arcangeli, Comp. Fl. Ital. 160 (1882).

Sickle medic is a bright yellow-flowered perennial herb with straight to sickle shaped pods. Similar in habit to lucerne (Fig. 12).

Vouchers

Grobbelaar 1068; *Prinshof Station* 1608; *Theron* 72.

4. **M. × hemicycla** *Grossh. (M. sativa × M. falcata). M. hemicycla* Grossh. in Zap. lauchno-prikl. Otd. tiflis Sada 4: 147 (1925). *M. sativa* L. subsp. × *hemicycla* (Grossh.) Gunn, U.S.D.A. Tech. Bull. 1574: 15 (1978).

A fertile hybrid with variegated or purple-tinged flowers and curved to C-shaped pods. Fig. 13.

Voucher

Moorwood 25642.

5. **M. intertexta** (*L.*) *Mill.*, Gard. Dict. edn 8, no. 4 (1768). *M. polymorpha* L. var. *intertexta* L., Sp. Pl. 780 (1753).

Yellow to orange-flowered annuals forming spherical to ovoid, 8–9, loosely appressed, glabrous burrs with interlocking appressed spines. Seeds black. A purple basal shield-shaped mark may be present. Hedgehog medic.

Voucher

Grobbelaar 974 (immature specimen, so some doubt about this identification).

6. **M. orbicularis** *(L.) Bart.*, Cat. Plante Siena: 60 (1776). *M. polymorpha* var. *orbicularis* L., Sp. Pl. 779 (1753).

Button medic is an omni-Mediterranean annual species apparently adventitious in central Europe but unsuccessful elsewhere. It has very characteristic smooth pods, which resemble a pile of stacked circular cushions. Seeds are minutely tuberculate. The radicle is almost as long as the cotyledons.

Voucher

Grobbelaar 1364.

7. **M scutellata** *(L.) Mill.*, Gard. Dict. edn 8, no. 2 (1768).

Snail medic is a hairy annual with large irregularly toothed stipules, 1–3 flowers and large unarmed spirally coiled snail-like pods.

Voucher

Grobbelaar 971.

8. **M. turbinata** *(L.) All.*, Fl. Pedem. 1: 315 (1785). *M. polymorpha* L. var. *turbinata* L., Sp. Pl. 780 (1753).

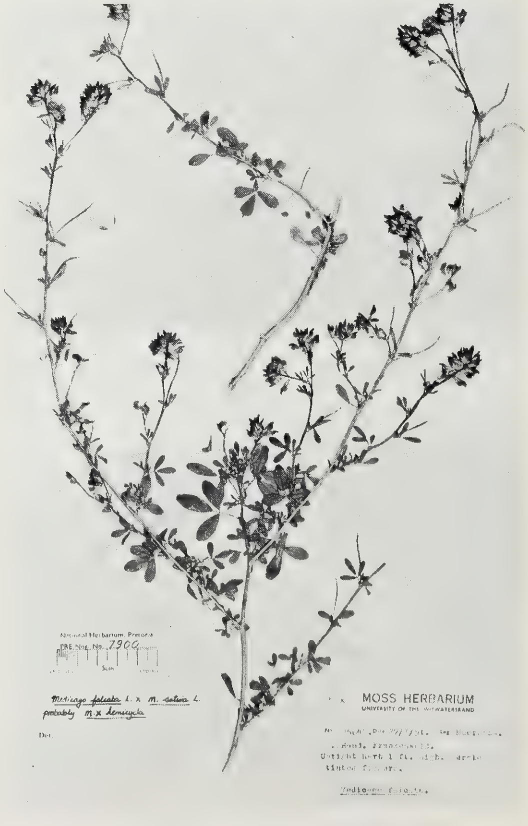
National Herbarium, Pretoria
PRE Neg. No. 7900
5cm
Medicago falcata L. x M. sativa L.
probably M. x hemicycla
MOSS HERBARIUM

FIG. 13—*Medicago* × *hemicycla* Grossh. *(Moorewood* s.n.)

The following specimens do not bear fruits and so are included here with a measure of doubt.

Vouchers

Grobbelaar 160, 169, 973.

Further information on these cultivated species may be found in Healy (1976), Gunn *et al.* (1978), McComb (1974) and Lesins *et al.* (1980).

UITTREKSEL

Vier species van Medicago: M. laciniata, M. polymorpha, M. sativa *en* M. lupulina *het in Suidelike Afrika genaturaliseerd geraak. Hulle morfologiese variasie en geografiese verspreiding word bespreek en 'n sleutel word voorsien.*

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Bothalia 14, 1: 37–44 (1982)

The genus *Melica* L. (Poaceae) in southern Africa

G. E. GIBBS RUSSELL* and R. P. ELLIS*

ABSTRACT

Two species are recognized in this revision of the genus *Melica.* Both species belong to the subgenus *Melica,* and are the only representatives of the genus in Africa south of the Sahara. Five species formerly recognized have been reduced to synonymy.

INTRODUCTION

In Species Plantarum (1753), Linnaeus described three species in *Melica,* all from the northern hemisphere. The first southern African species were described by Thunberg in the Prodromus of 1794, where he assigned six species to the genus, but in Flora Capensis of 1823 he correctly moved four of these to *Ehrharta,* leaving the two *Melica* species presently recognized. Additional species were described over the years by Schrader (1821), Lehmann (1821), Nees (1841) and Stapf (1900 and 1910), so that by the time of Flora Capensis, Stapf (1900) recognized six species. Following Stapf, Chippindall (1955) accounted for seven species, but gave a key to only the two Thunberg species, and implied doubt about the status of the other five, which are here reduced to synonymy.

Melica was not typified by its author (Linnaeus, 1754), and two proposals have been made for a lectotype. Nash in Britton & Brown (1913) put forward *M. ciliata* as the lectotype. Hitchcock & Green (1929) suggested instead that the Standard-species should be *M. nutans,* on the grounds that Linnaeus first used the generic name *Melica* in Flora Lapponica in 1737, and the species there was *M. nutans.* The Nash proposal can be superseded by the Hitchcock & Green proposal on the grounds that all the lectotypes set out in Britton & Brown (1913) were selected arbitrarily (Stafleu, 1978). The Index Nominum Genericorum accepts *M. nutans* as the lectotype species for the genus.

Melica is a classical name that was adopted by Linnaeus for this genus. Theophrastus applied it to an unknown species of *Sorghum,* and in Italy the name today is used for a kind of *Sorghum* with sweet juice (mel = honey).

Hempel (1970 and 1973) has divided *Melica* into subgenera and sections. Our two species both occur in subgenus *Melica, M. racemosa* in the section *Melica* and *M. decumbens* in the section *Beckeria* (Bernh.) Aschers. emend. Hempel. It is interesting to note that each of the three Linnaean species is the type of a different subgenus or section as recognized by Hempel. *M. nutans* is the type of subgenus *Melica* and section *Melica, M. ciliata* is the type of subgenus *Melica* and section *Beckeria,* and *M. altissima* is the type of subgenus *Altimelica. Melica* is thus one of the few Linnaean grass genera that has remained undivided to the present day.

POSITION OF *MELICA* IN THE POACEAE

There has been little controversy about the subfamily and tribal affinities of *Melica.* The genus has appeared for the past century in relatively the same position in most treatments, although the classification of the Poaceae has been changed drastically during that time. Bentham in Genera Plantarum (1883) classified *Melica* in series B Poaceae, tribus XI Festuceae, subtribus 6 Meliceae, along with the other genera *Heterachne, Anthochloa,* and *Diarrhena.* Modern systems, with more subfamilies, recognize the same affinities for *Melica.* Gould (1968), writing for North America, classified *Melica* in subfamily I Festucoideae, tribe 4 Meliceae, and included the genera *Glyceria, Catabrosia, Pleuropogon* and *Schizachne.* Tzvlev (1968) has classified the grasses of the USSR, with *Melica* in subfamily 2 Pooideae, tribe 15 Meliceae, with the genera *Schizachne* and *Pleuropogon.* For Africa, Clayton (1970) in the Flora of Tropical East Africa placed tribe XII Meliceae, in the Pooid subfamily, with only one genus from tropical Africa, *Streblochaete.* In an unpublished list of world grass genera (Clayton, 1980), he included six genera in the tribe, *Streblochaete, Lycochloa, Schizachne, Triniochloa, Anthochloa* and *Melica,* but placed *Diarrhena, Glyceria* and *Pleuropogon* in separate tribes. The only modern system in which Meliceae has been placed outside the Pooideae or Festuceae is that of Tateoka (1957), where it is included in the subfamily Arundoideae. However, he later moved the tribe, consisting of the genera *Glyceria, Pleuropogon, Schizachne, Streblochaete* and *Lycochloa,* to the Festucoideae (Tateoka, 1965).

DISTRIBUTION

A genus of about 70 species, *Melica* is widespread in temperate areas except Australia. The northern hemisphere distribution encircles the earth, north of the tropic of Cancer. The southern hemisphere distribution is disjunct from the northern hemisphere, with one area in South America and another in southern Africa. The southern African species are geographically the most isolated. The nearest species on the continent are in northern Algeria and Morocco, and the nearest in the southern hemisphere are in South America. (Hempel, 1970).

MORPHOLOGY

Both southern African species of *Melica* grow in compact many-stemmed clumps, with short thin rhizomes, which are buried as much as 150 mm. The culms may branch below the soil surface, so that in a large plant there is a tough net-like mass of rhizomes

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and culm bases. The leaf sheaths and blades are scabrous with fine retrorse hairs. In *M. decumbens* the leaf blades are always strongly scabrous. *M. racemosa* most often has scabrous leaf blades also, but sometimes the leaves may be glabrous or velvety, or with scattered hairs on the upper surface. This condition is so characteristic of *Melica* that the genus may be recognized in the field by the texture of the leaves even when the plants are not flowering. In the past taxa have often been confused because of differences in the appearance of the leaf blades on herbarium specimens. In nature, the plants usually have their leaf blades expanded with the lamina held flat or slightly curved upward at the margins and the base rounded. However, as soon as the plants are damaged the blades quickly roll up so that they appear nearly filiform, and the rounded base is not obvious. For this reason, specimens of the same taxon may appear quite different on a herbarium sheet, depending on how quickly they were pressed after collection.

The inflorescence is a narrow, raceme-like panicle which overtops the leaves. The abundant lemma hairs glisten in the sun and the shining inflorescences make the plants conspicuous when in flower. The spikelets of both species are similar in structure and appearance, differing mainly in size and in location of the hairs on the lemmas. They are awnless, somewhat laterally compressed and normally bear two fertile florets, the lower larger than the upper. At the end of the rhachilla is a knob-like body composed of two or three small empty lemmas which are closely rolled into each other. This clavate structure is an important character for distinguishing the genus. The glumes are boat-shaped, glabrous, and papery in texture, with raised nerves. They are about the same length as the spikelet, being sometimes slightly shorter and sometimes slightly longer. The lemmas are firmer than the paleas, with more nerves, and provide the main distinguishing character between the southern African species. In *M. racemosa* the hairs arise only from the lateral nerves, leaving the back of the lemma glabrous, whereas in *M. decumbens* there are hairs on and between the nerves over the entire lemma. The paleas are sharply folded back along the two nerves, so that the margin of the palea outside the nerve is pressed against the back of the palea, and clasps the immature anthers and stigmas.

The lower floret is always hermaphrodite, but the upper one may rarely be staminate, especially under adverse growing conditions. *Melica* is protandrous, and the anthers are usually shed, leaving the filaments behind, before the stigmas are exserted. The lodicules are short, thick and rounded. When the fruit is mature the florets dis-articulate at the base, and the portion of the rhacilla that bore the floret above remains pressed against the palea. The glumes are deciduous with the florets, an unusual condition in a festucoid grass. The entire spikelet may act in wind dispersal of the seed, with the lemma hairs catching the air currents as a sail.

LEAF BLADE ANATOMY

The Pooideae can be briefly diagnosed, on the basis of leaf anatomy, as follows: micro-hairs absent; silica bodies horizontally elongated square to oblong, usually with crenate or sinuous outlines; stomatal subsidiary cells parallel-sided; intercostal long cell walls often straight and not sinuous; papillae very rare; double bundle sheaths around first order vascular bundles; chlorenchyma cells not radiately arranged around the vascular bundles; bulliform cells not associated with colourless cells to form deeply penetrating fans; all vascular bundles accompanied by sclerenchyma; lateral cell count greater than four (Hattersley & Watson, 1975); non-Kranz leaf anatomy and C_3 photosynthesis.

The leaf anatomy of *Melica* is typical of this pooid (festucoid) type and *M. racemosa* and *M. decumbens* (Figs 1 & 2) conform exceptionally closely to the anatomical diagnosis for this subfamily. The epidermal and leaf blade anatomical attributes used in the above diagnosis of the festucoid leaf type are all present in combination in both the South African species of *Melica* except that both species lack abaxial stomata (Fig. 2a & c) and so stomatal subsidiary cell shape cannot be recorded. The intercostal long cells have minutely sinuous periclinal walls (Fig. 2b & d).

Slightly sinuous long cell walls are known from other festucoid grasses, such as *Mibora minima* L.) Desv. (Clifford & Watson, 1977), and, consequently, little emphasis is attached to this minor difference from the festucoid norm. Intercostal long cell shape and arrangement is nevertheless characteristically festucoid. Transverse sections of *Melica* leaves (Fig. 4c & e) clearly illustrate stomata in the adaxial epidermis. These transverse sections of stoma show that the stomatal apparatus is overlapped by interstomatal cells. From this observation it can be inferred that *Melica* has typical, parallel-sided festucoid stomata because only this type is overlapped by the adjoining interstomatals (Watson & Johnston, 1978). In addition, *M. ciliata* L. and *M. uniflora* Retz, both described by Metcalfe (1960), lack abaxial stomata but *M. altissima* L. has parallel-sided abaxial subsidiary cells. For these reasons neither of these slight structural deviations is considered significant and, therefore, the anatomy of *M. decumbens* and *M. racemosa* is considered to be typically festucoid.

Melica is non-Kranz. This has been confirmed by the carbon isotope ratios of *M. altissima* (−28%) (Troughton *et al.*, 1974) and *M. mutica* Walt. (−26,0%) (Smith & Brown, 1973). These $S^{13}C$ values are typical of plants possessing the C_3 photosynthetic pathway and it can consequently be concluded that *M. decumbens* and *M. racemosa* are C_3 plants as are all members of the Pooideae (= Festucoideae) (Waller & Lewis, 1979).

Leaf anatomy, therefore, corroborates the classification of *Melica* in the Pooideae and there appears little doubt that the genus belongs in this subfamily. The leaf anatomy is so typically festucoid that, on the anatomical evidence from *M. racemosa* and *M. decumbens,* there appears little need for the recognition of the tribe Meliceae. On anatomical grounds the southern African *Melica* species could quite satisfactorily be placed near genera such as *Festuca* or *Helictotrichon*. However, lodicule and chromosomal differences appear to justify maintaining a separate tribe for *Melica* and its allies (Decker, 1964) and suggest that the Meliceae is phylogenetically fairly distant from the Festuceae and Aveneae (Tateoka, 1965). The abundant papillae mentioned by Decker (1964) as often being present on grasses of the Meliceae were observed on neither of the *Melica* species studied, nor on *Streblochaete longiarista* Pilg., another member of the Meliceae. Papillae are also not mentioned in descriptions of *Melica* anatomy of Metcalfe (1960). Chains of costal globose papillae, as well as abundant, oblique, adaxial intercostal papillae appear to be characteristic of other genera of the Meliceae such as *Glyceria* and *Pleuropogon* (Metcalfe, 1960), but they are absent in *Melica*. Papillae are very rare in the Pooideae (Clifford & Watson, 1977) which indicates that some of the genera of the Meliceae are phylogenetically distant from *Festuca* and its allies.

The only other South African grass placed in the Meliceae is *Streblochaete longiarista* (Tateoka, 1965). There is nothing in the leaf anatomy to suggest that this grouping is artificial. The leaf of *S. longiarista* has a well-developed midrib and keel and the leaf is thinner and wider than the leaves of *M. racemosa* and *M. decumbens*. In all other respects, including the absence of abaxial stomata, the leaf structure is very similar to that of *Melica* species. The thinner leaf is undoubtedly an adaptation to the shady forest habitat that *S. longiarista* favours (Chippindall, 1955). It is of interest to record that the transverse leaf sections of *M. uniflora*, as illustrated by Lewton-Brain (1904) and Burr & Turner (1933), are practically identical to those of *Streblochaete*. Furthermore, *M. uniflora* is a species of shady places (Lewton-Brain, 1904) and, like *S. longiarista*, has thin leaves with poorly developed adaxial ribs, widely spaced vascular bundles with very little associated sclerenchyme and a distinct midrib. In all these respects *M. uniflora* is more similar to *S. longiarista* than to *M. racemosa* and *M. decumbens*.

Anatomically *M. racemosa* and *M. decumbens* are very similar in all respects. The leaves of *M. racemosa* tend to be slightly thinner than those of *M. decumbens* (Fig. 1b & e). This is not a consistent difference, however, and merely appears to reflect a trend. It is the only anatomical difference detected between the two species and indicates their close relationship — an observation which agrees with the morphological evidence.

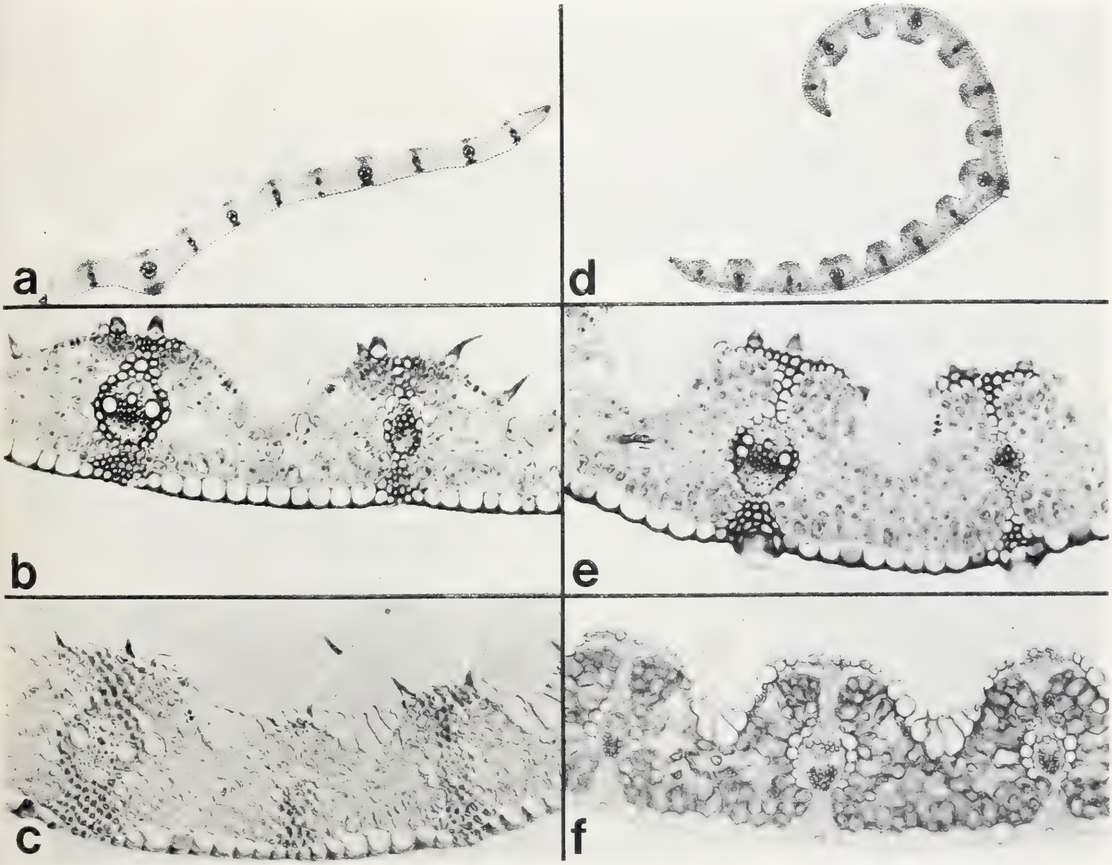

FIG. 1.—Leaf transverse sections of *Melica racemosa* and *M. decumbens*. a–c, *M. racemosa;* a & b, *Ellis* 1246; a, × 100; b, × 400; c, *Ellis* 593, × 400, interference contrast optics; d–f, M. decumbens; d, *Ellis* 2095, × 100; e, *Ellis* 1814, × 400; f, *Ellis* 2095, × 400.

Specimens examined:

Melica racemosa

TRANSVAAL.—2528 (Pretoria): Poison garden, National Botanical Garden (−CA), *Ellis 1246, 1815.*

CAPE.—3320 (Montagu): Barrydale (−DC), *Ellis 1204.* 3325 (Port Elizabeth): Summerstrand (−DC), *Ellis 605.* 3326 (Grahamstown): Grahamstown Nature Res. (−BC), *Ellis 593.*

Melica decumbens

TRANSVAAL.—2528 (Pretoria): Poison garden, National Botanical Garden (−CA), *Ellis 1245, 1814.*

O.F.S. — 2926 (Bloemfontein): Naval Hill (−AA), *Van Heerden 86.* 3025 (Colesberg): 70 km N. of Colesberg (−CA), *Smook 3190.* 3026 (Aliwal North): Rouxville (−BD), *Ellis 2095.*

MELICA

Melica *L.*, Sp. Pl. 66 (1753); Thunb., Prodr. 1: 21 (1794); Fl. Cap. edn. 2: 111 (1823); Nees, Fl. Afr. Austr. 417 (1841); Benth. in J. Linn. Soc., Bot. 19: 119 (1882); Hack. in Natürl. Pfl. Fam. 2,2: 70 (1887), True Grasses 157 (1896); Stapf in F.C. 7: 684 (1900); Bews, Grasses & Grasslds S. Afr. 76 (1918); Chippind. in Meredith, Grasses & Past. S. Afr. 73 (1955); Gordon-Gray in Ross, Fl. Natal 96 (1972); Loxton in R. A. Dyer, Gen. 2: 866 (1976). Type species: *M. nutans* L.

Caespitose perennials with short, woody, deeply buried rhizomes and numerous simple or rarely branched culms. *Leaves* with sheaths overlapping; ligule a delicate hyaline membrane; blades expanded or rolled, usually slightly auriculate at base. *Inflorescence* an erect terminal raceme or narrow raceme-like panicle, often one-sided. *Spikelets* barely compressed laterally, borne on short pedicels with thickened tips, often nodding; glumes equal or unequal, narrowly to broadly ovate, ± equalling the florets, 3−7 nerved, papery, glabrous, white or tinged with purple. *Florets* 3−6, the basal 2 (rarely 1 or 3) bisexual, the upper 2−3 sterile, reduced to empty lemmas tightly compacted into an oval body borne at end of rhachilla; lemmas of bisexual florets slightly firmer than glumes, 7−9-nerved, with long shining silvery hairs; paleas of bisexual florets obovate, ciliate on nerves.

KEY TO THE SPECIES

Lemmas of bisexual florets hairy only on the margins, glabrous or slightly scabrous on the back; lemmas of sterile florets glabrous or with a few hairs; spikelets 5−9 (−11) mm long.......... 1. *M. racemosa*

Lemmas of bisexual florets hairy on the back and margins; lemmas of sterile florets usually hairy; spikelets 10−15 mm long.......... 2. *M. decumbens*

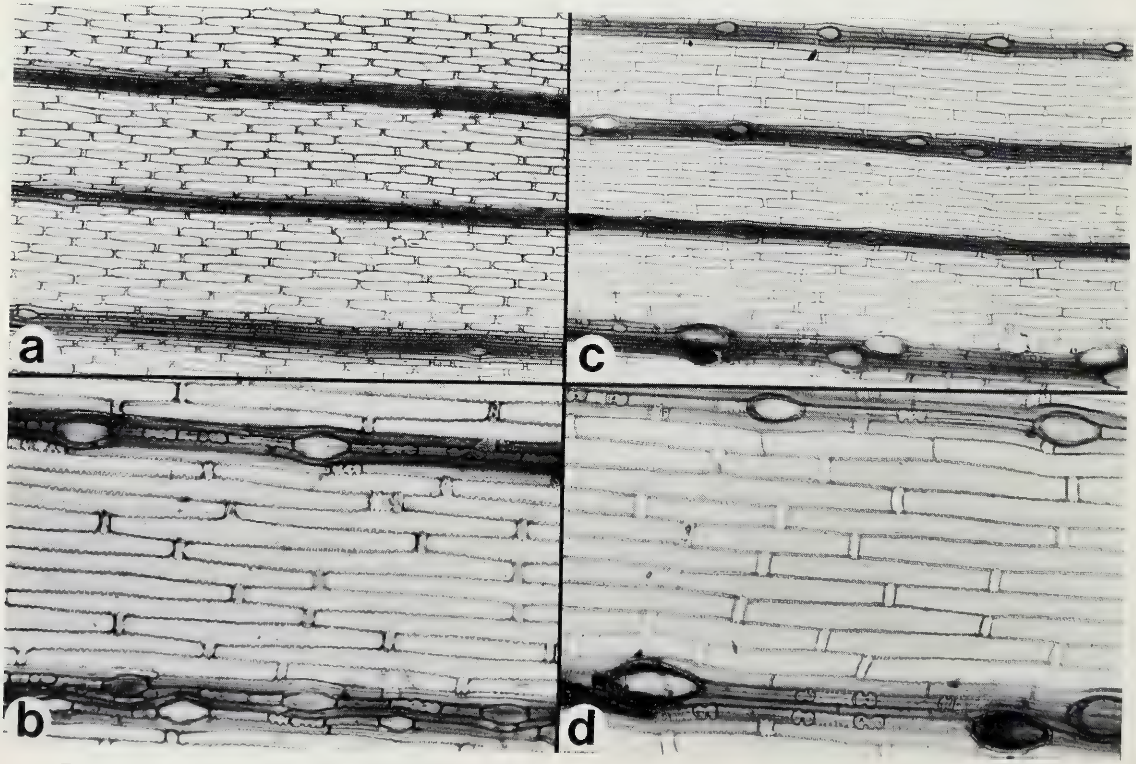

FIG. 2.—Abaxial epidermal preparations of *Melica racemosa* and *M. decumbens*. a & b, *M. racemosa;* a, *Ellis 605*, × 160; *b, Ellis* 1815, × 400; c & d, *M. decumbens, Ellis* 2095; c, × 160; d, × 400.

1. **Melica racemosa** *Thunb.*, Prodr. 1: 21 (1794); Stapf in Fl. Cap. 7: 687 (1900); Chippind. in Meredith, Grasses & Past. S. Afr. 74 (1955); Gordon-Gray in Ross, Fl, Natal 96 (1972). Type: Cape, *Thunberg* s.n., Herb. no. 2173 (UPS, holo.; microfiche in PRE!).

M. decumbens Thunb. var. *racemosa* (Thunb.) Kuntze, Rev. Gen. 3: 356 (1898).

M. caffrorum Schrad. in Goett, Anz. Ges. Wiss. 3: 2072 (1821). Type: Hesse in Herb. Schrad. (LE, holo!, GOET, iso.!; photocopies in PRE!).

M. caffrorum Schrad. var. *elatior* Nees, Fl, Afr. Austr. 418 (1841). Type: Cape, *Ecklon* 803 (holo., apparently lost). Cape, in collibus ad Grahamstown, alt. 1 000–2 000 ft. (Albany), *Drège* s.n. (K. lecto; photo. in PRE!).

M. ovalis Nees, Fl. Afr. Austr. 417 (1841); Stapf in F.C. 7: 686 (1900); Chippind. in Meredith, Grasses & Past. S. Afr. 75 (1955). Type: Cape, Queenstown, Stormberg Range, 5 000–6 000 ft., *Drège* s.n. (K, iso.; photo, and fragment in PRE!).

M. bolusii Stapf in Fl. Cap. 7: 686 (1900); Chippind. in Meredith, Grasses & Past. S. Afr. 74 (1955). Type: Cape, Graaff-Reinet, in sylvestris in monte Compassberg, 8 300–8 500 ft., *Bolus* 1985 (K, holo.; photo in PRE!).

M. pumila Stapf in Fl, Cap. 7: 686 (1900); Chippind. in Meredith, Grasses & Past. S. Afr. 75 (1955). Type: Cape, Prince Albert, near Weltevrede, *Drège* s.n. (K, holo.; photo in PRE!).

M. brevifolia Stapf in Kew Bull. 1910: 131 (1910); Chippind. in Meredith, Grasses & Past. S. Afr. 75 (1955). Type: Cape, Great Winterberg, mountainside, 7 400 ft., *Galpin* 5614 (K, holo.; photo in PRE!).

M. decumbens sensu Gordon-Gray in Ross, Fl. Natal 96 (1972), non Thunb.

A tufted perennial with simple or rarely branched culms 300–500 mm high. *Leaf sheath* usually scabrous; ligule a truncate membrane 1–2 mm long; blade erect, expanded or rolled, often scabrous, but sometimes smooth with scattered long hairs or velvety on upper surface, 40–300 mm long and 1,5–5 mm across. *Spikelets* 5–9 (–11) mm long, whitish. *Florets:* bisexual florets 2 or 1, lemmas with

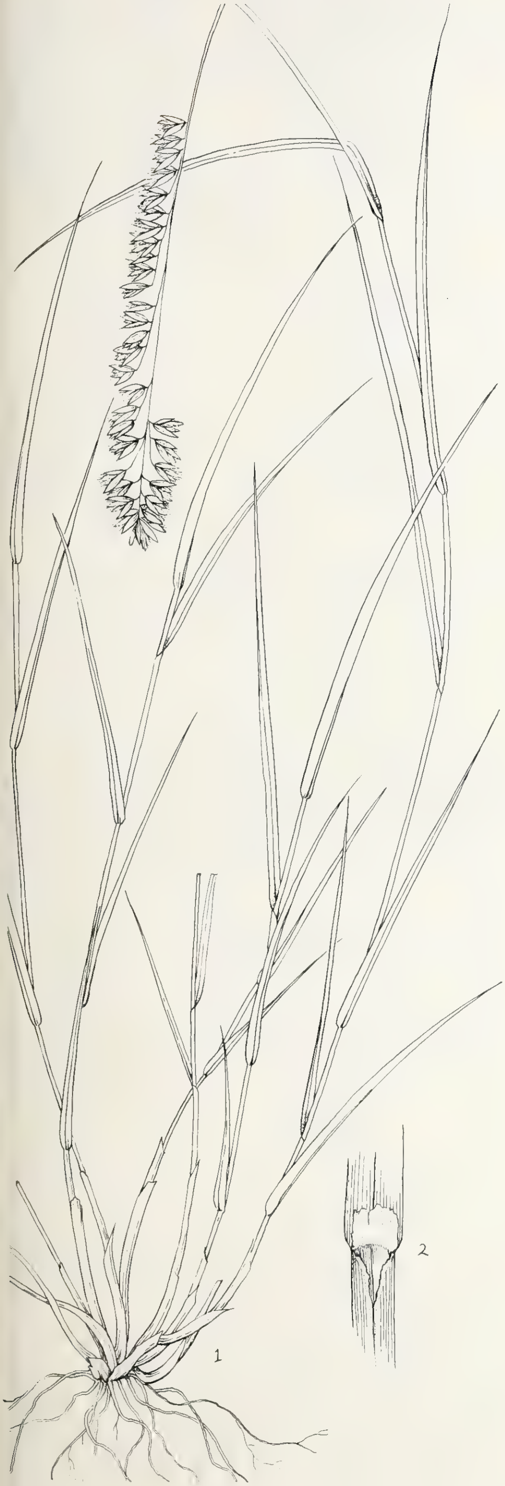

FIG. 3.—*Melica racemosa.* 1, habit, × ½; 2, ligule, × 3; drawn from *Loxton* 227 (PRE).

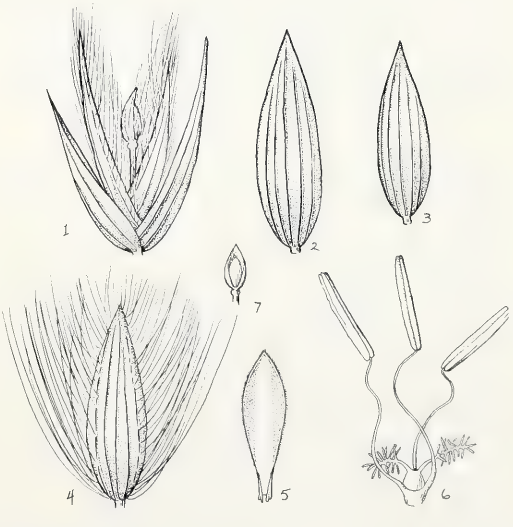

FIG. 4.—*Melica racemosa.* 1, spikelet, × 5; 2, upper glume; × 5; 3, lower glume, × 5; 4, lemma of lower floret, × 5; 5, palea of lower floret, × 5; 6, androecium and gynoecium, × 7; 7, sterile lemmas, × 5; drawn from *Loxton* 227 (PRE).

long white hairs around the margins, glabrous on back; sterile lemmas glabrous or with a few sparse hairs. Figs 3 & 4.

M. racemosa occurs from the south-western Cape to Natal, Lesotho and the southern and eastern Orange Free State, and is rare in the eastern Transvaal (Fig. 5). It often grows among rocks on steep hill and mountain slopes and also in savanna and fynbos, at the edges of bushclumps and in grassland, and rarely between seaside dunes and in forest clearings.

TRANSVAAL.—2531 (Komatipoort): Barberton (−CC), *Thorncroft 21.*

O.F.S. — 2727 (Kroonstad): Kroonstad, near Vals River (−CA), *Pont 570.* 2828 (Bethlehem): Near top of Sentinel at Mont-aux-Sources (−DB), *Smook 1220.* 2925 (Jagersfontein): Samara, Fauresmith (−CB), *Brueckner 960.*

NATAL.—2831 (Nkandla): Shongweni Dam, Camperdown (−AA), *Morris 905.* 2832 (Mtubatuba): Hlabisa, Hluhluwe Game Reserve (−AA), *Guy 40; Ward 2805.* 2929 (Underberg): Sani Pass (−CB), *Du Toit 2317.* 3030 (Port Shepstone): Isipingo Flats, former floodplain of Umlazi River (−BB), *Ward 5866.*

LESOTHO.—2928 (Marakabei): Semongkong, rocky slope (−CC), *Schmitz 4093.* 2929 (Underberg): Sehlabathebe National Park (−CC), *Beverly 794.*

CAPE.—3026 (Aliwal North): Tussen-die-Rivieren Nature Reserve (−AC), *Edwards 4179.* 3927 (Lady Grey): Barkly East (−DC), *Greyvenstein 10.* 3119 (Calvinia): Van Rhyn's Pass, upper slopes (−AC), *De Winter & Verdoorn 9022.* 3224 (Graaff-Reinet): 10 km west of Graaff-Reinet (−BC), *Gibbs Russell, Robinson & Herman* 291. 3226 (Fort Beaufort): Gaika's Kop, Amatola Mts (−DB), *Gibbs Russell 3519. 3228 (Butterworth): Kentani (−AD), Pegler 1392.* 3318 (Cape Town): Camps Bay (−CD), *Wolley Dod 3106.* 3320 (Montagu): Streambed, Bantams Karoo, Laingsburg (−BB), *Compton 12160.* 3325 (Port Elizabeth): Groendal Wilderness Res. (−CA), *Scharf 1973;* Coastal dunes, Humewood, Port Elizabeth (−DC), *Dahlstrand 155.* 3421 (Riversdale): Riversdale Nat. Res. (−AB), *Taylor 7830.* 3422 (Mossel Bay): Sedgefield, coastal vegetation (−BB), *Morze 2260.*

M. racemosa is a very variable species that includes entities described as separate species in the past. Characters used to separate these taxa such as culm length, leaf length, degree of expansion and vesture, spikelet length, glume shape and length, and number of bisexual florets vary independently and are not generally correlated. The reduction of bisexual florets to one appears to be related to hostile environments such as high altitudes and sea dunes. Specimens from Natal tend to have spikelets 9−11 mm long, overlapping into the size range of *M. decumbens,* and were included in that species by Gordon-Gray in Flora of Natal (1972), as exemplified by *Ward* 2805. They are assigned here to *M. racemosa* because of the glabrous backs to the lemmas. Large size differences in the spikelets and general variability of the material suggests that chromosome races, may be present and a cytogenetics study could prove useful.

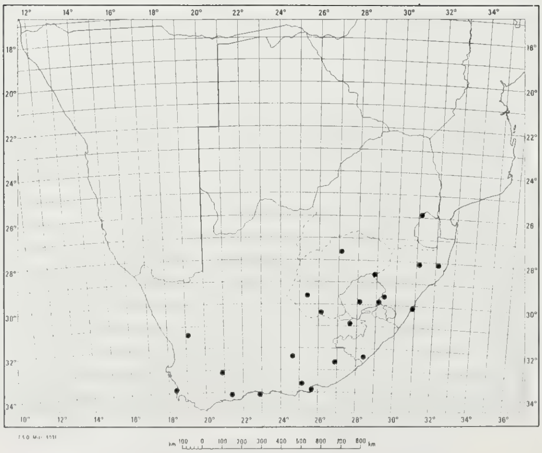

FIG. 5.—Distribution of *Melica racemosa.*

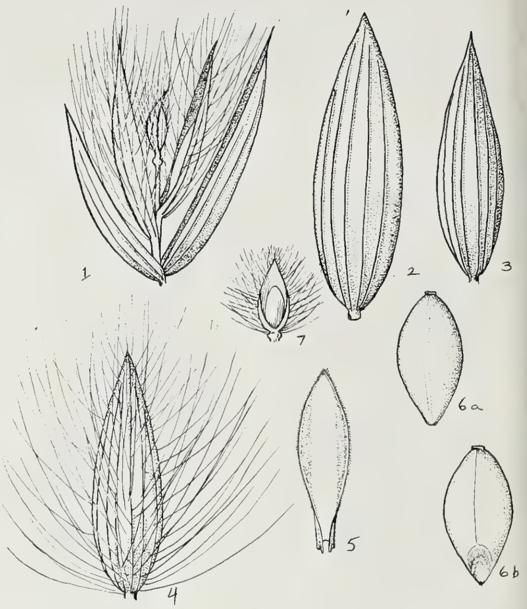

FIG. 6.—*Melica decumbens.* 1, spikelet, × 2; 2, upper glume, × 2; 3, lower glume, × 2; 4 lemma of lower floret, × 5; 5, palea of lower floret, × 2; 6a, caryopsis, abaxial, × 10; 6b, caryopsis, adaxial, × 10; 7, sterile lemmas, × 2; drawn from *Gill* 40 (PRE).

2. **Melica decumbens** *Thunb.,* Prodr. 1: 21 (1794); Stapf in Fl. Cap 7: 687 (1900); Chippind. in Meredith, Grasses & Past. S. Afr. 75 (1955); Gordon-Gray in Ross, Fl. Natal 96 (1972). Type: Cape, *Thunberg,* s.n., Herb. no. 2166 (UPS, holo.; microfiche in PRE!).

M. caffrorum Schrad. var. *decumbens* (Thunb.) Nees, Fl. Afr. Aust. 418 (1841).

M. dendroides Lehm., Pugill. Pl. 2: 39 (1828). Type: Cape, *Lehmann* s.n. (S, lecto.!; photo. in PRE).

M. neesii Stapf in Fl. Cap. 7: 687 (1900); Chippind. in Meredith, Grasses & Past. S. Afr. 75 (1955). Type: Cape, Prince Albert, near Weltevrede, *Drège* 752 in Herb. Lüb. (K. holo.; photo in PRE!).

A tufted perennial with simple culms 300−500 mm high. *Leaf sheaths* scabrous; ligule a truncate membrane 1—2 mm long; blade erect, usually rolled, strongly scabrous, 20−200 × 1,5−3,5 mm. *Inflorescence* a narrow 1-sided panicle of 1−5 racemes to 120 mm long. *Spikelets* 10−15 mm long, glumes frequently purple-tinged. *Florets:* bisexual florets 2; lemmas with long white hairs on the entire back, often tuberculate between veins; sterile lemmas hairy. Fig. 6.

The distribution of *M. decumbens* is centered in the eastern Cape and Orange Free State extending into the northern Cape and Lesotho (Fig. 7). It is known from the south-western Cape only by the type specimen. It grows on hillsides, koppies and mountainsides, often among rocks or in the shade of trees, and occasionally on roadsides and along railway lines.

O.F.S.—2727 (Kroonstad): 4 miles SSE of Kroonstad (−CA), *Scheepers 1540.* 2826 (Brandfort): Krugersdriftdamnatuurreservaat (−CC), *Muller 1544.* 2827 (Senekal): Willem Pretorius Game Reserve (−AC), *Van Zinderen Bakker 1158.* 3025 (Colesberg): Along roadside between Philippolis and Springfontein (−BC), *De Winter 8692.* 3027 (Lady Grey): Zastron, Aasvoëlberg, (−AC) *Smook & Gibbs Russell 2288.*

LESOTHO.—2927 (Maseru): Mamathes, on slopes above cannibal's cave (−BB), *Jacot Guillarmod 856.* 3027 (Lady Grey): 10 km from Quthing (−BC), *Du Toit 2694A.*

CAPE.—2823 (Griekwastad): Campbell, erf near village (−DC), *Wilman 1415.* 2824 (Kimberley): Koopmansfontein, Agricultural Research Station. (−AA), *Nursey 68.* 3024 (De Aar): Rolfonteinnatuurreservaat (−BB), *Jooste 143.* 3025 (Colesberg): Tussen-die-Riviere Wildtuin (−BD), *Roberts 5324.* 3026 (Aliwal North): Radio Springs (−DA), *Coetzee A33.* 3124 (Hanover): Lootsberg, Middelburg Dist. (−DD), *Gill 40.* 3126 (Queenstown): mountains near Fincham's Nek (−DD), *Galpin 2373.* 3222 (Beaufort West): Mountain View Farm, Nieuwveld Mts (−BD), *Gibbs Russell, Robinson, Herman & Downing 133.* 3225 (Somerset East): Bruintjies Hoogte (−CB), *without collector* 29-3-21. 3226 (Fort Beaufort): Alice, (−DD), *Giffen 691.*

M. decumbens has been known as 'dronkgras' since the time of Thunberg, and is suspected of being poisonous to cattle, horses and donkeys. Affected animals stagger as if intoxicated.

Ehrharta villosa may be confused with *M. decumbens.* The species are easily distinguished by the aristate lemma tips in *E. villosa,* and the presence of congested sterile lemmas at the end of the rhachilla in *Melica.*

SPECIES EXCLUDED

Melica festucoides Licht. ex Roem & Schult. in Roem. & Schult., Syst. Veg. 2: 530 (1817) = *Pogonarthria squarrosa* (Licht.) Pilg.

Melica festucoides Willd. ex Steud., Nom. Bot. 2: 2 (1841) = *Pogonarthria squarrosa* (Licht.) Pilg.

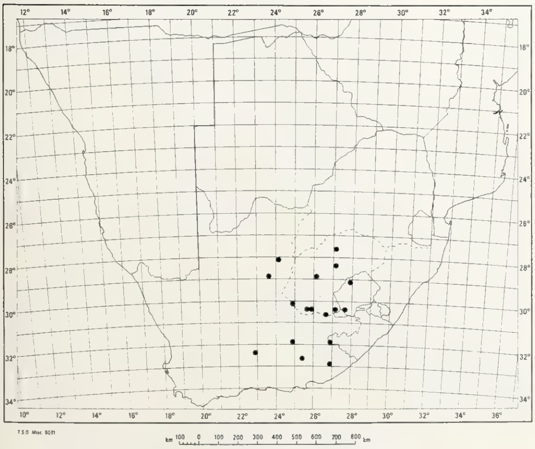

FIG. 7.—Distribution of *Melica decumbens.*

Both these names are based on the same type, a Lichtenstein specimen in the Willdenow herbarium. This specimen is clearly *Pogonarthria squarrosa.*

ACKNOWLEDGEMENTS

Claire Smith made the drawings of the habit and spikelet structure.

UITTREKSEL

Twee spesies van die genus Melica *word in hierdie hersiening erken. Beide die spesies behoort tot die subgenus* Melica, *en hulle is die enigste verteenwoordigers van die genus in Afrika suid van die Sahara. Vyf spesies, voorheen erken, word tot sinonieme verlaag.*

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The subspecies of *Pelargonium cucullatum* (Geraniaceae)*

B. VOLSCHENK, J. J. A. VAN DER WALT and P. J. VORSTER**

ABSTRACT

Pelargonium cucullatum (L.) L'Hérit. is shown to consist of three infraspecific taxa, which are given subspecific ranking under the names *P. cucullatum* subsp. *cucullatum*, subsp. **tabulare** Volschenk and subsp. **strigifolium** Volschenk. It is also shown that *P. angulosum* (Mill.) L'Hérit. (*Geranium angulosum* Mill.) is synonymous with *P. cucullatum* subsp. *cucullatum*, but that the name *P. angulosum* has been misapplied for many years to subsp. *strigifolium*. The latter was formerly known as *P. acerifolium* L'Hérit., non *Geranium acerifolium* Cav.

Pelargonium cucullatum (L.) L'Hérit. is a conspicuous and well-known species. It was first collected in 1672 by the Dutch botanist Paul Hermann of Leiden, probably on the slopes of Table Mountain where it is still abundant. The first record of its introduction into cultivation in England was that of Bentick in 1690. Harvey (1860) reported that it was used for ornamental hedgerows in Cape Town during his stay from 1838 to 1840. Horticulturally it is an important species which has been used extensively in hybridization, especially in the breeding of the 'regal' cultivars.

The identity and circumscription of *P. cucullatum* is important, as Van der Walt (1979) designated it as the lectotype species of the genus *Pelargonium.*

P. cucullatum in its original circumscription consisted of two taxa. The first taxon has leaves which are dentate but not incised and grows against the north-western, western and southern slopes of the Cape Peninsula as well as near Saldanha Bay. The second taxon has angularly incised leaves and occurs on the eastern side of the Cape Peninsula, on the eastern side of False Bay, and eastwards along the coast as far as the vicinity of Gansbaai. It always grows close to the beach. In both taxa the leaves are villous and soft to the touch. It was found that a third taxon, *P. acerifolium* L'Hérit. (commonly but erroneously known as *P. angulosum),* has such a close morphological resemblance to *P. cucullatum* that we do not consider it justified to afford them separate specific status. In this taxon the leaves are angularly incised, strigose and harsh to the touch. No structural differences could be detected between the flowers of the three taxa although the petals of *P. acerifolium* are often light pink instead of pinkish purple. As can be expected from the different textures of the indumentum, there is a difference in the shape of the individual trichomes on the leaves. Hence in *P. acerifolium* the trichomes are relatively short, broad-based and curved, whereas in the other two taxa the trichomes are conspicuously long, slender and straight.

A complete anatomical study was made of the young stems, petioles and laminae. The only differences that we noted between the three taxa are the presence of a central fibrous column in the central vascular bundle of the petiole of the first two taxa enumerated above (but absent in the third); and the arrangement of the guard cells of the stomata which are raised above the surface of the epidermis in the first two taxa, but are level with the surface of the epidermis in the third taxon.

We also examined the pollen grains of all three taxa with a light- and a scanning electron microscope, but could detect no difference between them.

Cuttings as well as field-collected seed of all three taxa were grown side-by-side in Stellenbosch to determine whether the differences which we observed were environmentally induced. We found that the plants retained their respective characters under these conditions. From this we conclude that the differences are genetically fixed.

It is our considered opinion that the degree of morphological similarity between the three taxa is of such a magnitude that we must regard them as conspecific. Nevertheless the differences in leaf shape and indumentum are striking, and are linked to an allopatric distribution which suggests a high degree of spatial genetical isolation between them. For these reasons we regard them as three separate subspecies of the same species to which the name *P. cucullatum* applies.

We interpret Linnaeus's original description as follows. Firstly, that the epithet *cucullatum* sensu stricto applies to the beach-hugging subspecies with incised, villous leaves. Secondly, that the subspecies with dentate, non-incised, villous leaves, found against the western, north-western and southern slopes on the Cape Peninsula be designated subsp. *tabulare* Volschenk, and finally that the former *P. acerifolium* be given a new name, subsp. *strigifolium* Volschenk.

The total combined distribution range of the three subspecies does not exceed about 220 km from west to east, and the three subspecies at places occur in close proximity to one another. It may seem unusual for three subspecies to occur in such a small area, but we would like to point out that this area is well-known for the the diversity of its flora. It is a mountainous area with deep intervening valleys in a region where great differences in climate and environmental conditions occur over short distances. This rugged topography provides effective barriers against migration and gene flow. Thus subsp. *cucullatum* occurs in cool situations near the beach mostly against east- or south-facing slopes (but west-facing immediately east of False Bay), on sandy and well-drained soil under a rainfall regime of 400–800 mm per annum. Subsp. *tabulare* occurs under a range of environmental conditions, from the dry, hot, west-facing slopes on the Cape Peninsula to cool moist conditions towards the tip of the Peninsula and on its east-facing slopes with an annual rainfall varying from 200 to 1 000 mm. The environmental conditions at Saldanha Bay where this subspecies also grows are probably more or less similar to those on the Cape Peninsula. Our impression is that subsp. *tabulare* can exist under conditions as moist as those under which subsp. *cucullatum* thrives, but that it can also survive in much hotter and drier situations. It occurs from near the beach to altitudes as high as 500 m. Subsp. *strigifolium* is essentialy montane and occurs further inland at altitudes of 300–900 m, experiencing an annual rainfall of 600–1 000 mm per annum. It is found on a variety of soils derived from sandstone, shale, tillite, granite and granofir, and plants experiencing the lower end of the rainfall range are often found on heavy soils. Whereas the habitat of subsp. *strigifolium* can become very wet during the winter months, it is drier during summer than the habitats of either subsp. *cucullatum* or subsp. *tabulare,* where the air is moist throughout the year due to their close proximity to the sea. All three subspecies occur in fynbos.

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*Forms part of an M.Sc. thesis submitted by the first-named author to the University of Stellenbosch.

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The present-day distribution areas of the three subspecies are not all continuous (Fig. 1). The main concentration of subsp. *cucullatum* is east of False Bay, but a few populations also occur on the Peninsula immediately west of False Bay but separated by a distance of about 35 km. This is not much, but as this subspecies is conspicuously absent on the intervening lowlands, it is assumed that the two concentrations are genetically isolated from each other. Subsp. *tabulare* is concentrated on the Cape Peninsula, but there are also a few populations around Saldanha Bay, separated by a break of about 90 km from the Peninsula concentration. In the case of subsp. *strigifolium,* it is unclear whether the disjunctions shown in Fig. 1 are real, or due only to imperfect collecting. It is nevertheless certain that it does not occur below about 300 m.

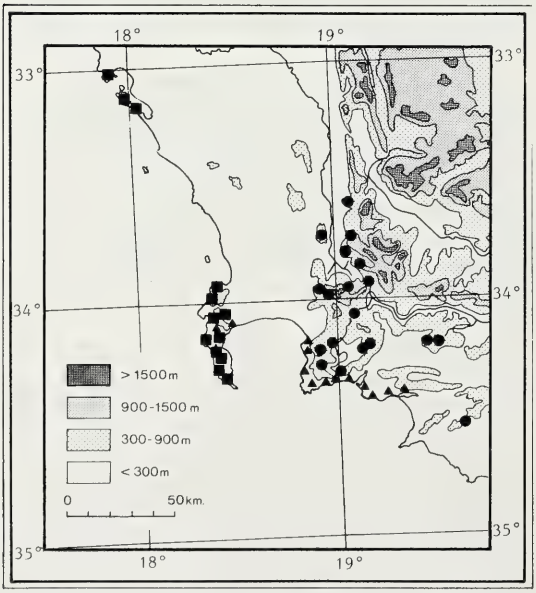

FIG. 1.—*Pelargonium cucullatum* (L.) L'Hérit. Map of the extreme south-western portion of the Cape Province, indicating the known geographical distribution of the three subspecies. ▲, subsp. *cucullatum*; ■, subsp. *tabulare*; ●, subsp. *strigifolium.*

The seeds of *P. cucullatum* are dispersed by wind, but their aerodynamic properties are such that it is unlikely that they are spread more than a few metres from the parent plant. For this reason it seems probable that the disjunct concentrations of the three subspecies are relics from a former much wider distribution. This is supported by evidence of past climatic fluctuations cited below.

Investigations by Brain & Meester (1964) indicated that the pattern of rainfall changes in southern Africa followed a cyclical sequence since the Plio-Pleistocene (1–2 million years ago) with three wet periods (pluvials) during which the rainfall may have been 150% higher than at present. It is conceivable that during one or more of these pluvials, conditions were moist enough along the west coast to enable subsp. *tabulare* to occupy a continuous area between Cape Point and Saldanha Bay. During the inter-pluvial this subspecies would have died out in the intervening area with only the present two relic populations surviving where conditions were still favourable for its continued existence. The same hypothesis could explain the present disjunct distribution of subsp. *cucullatum,* with the break in distribution afforded by the drier Cape Flats; as well as the confinement of subsp. *strigifolium* to mountainous areas, moister than the intervening areas. It is possible that during a pluvial the intervening areas were moist enough for the subsp. *strigifolium* to occupy a continuous area, but that when it became drier and conditions at lower altitudes became unsuitable for the survival of this subspecies, populations were left stranded on isolated masses of higher land.

The environmental differences experienced by the three subspecies, and even more so their environmental requirements, are still imperfectly understood, and much data remain to be gathered. All three appear to be quite adaptable when cultivated, and the restricted nature of their natural environment is perhaps to be sought in subtle moisture differences affecting seed germination.

Pelargonium cucullatum (*L.*) *L.'Hérit.* in Ait., Hort. Kew. edn 1, 2: 426 (1789). Type: Africa, without precise locality, specimen in Hort. Cliff. 345.17 (BM, lecto., here designated!) (Fig. 2).

Erect, perennial shrub, 1–2 m high, with a taproot system and a series of underground runners giving rise to aerial shoots at intervals. *Branches* herbaceous, becoming woody at base with age, 6–10 mm in diameter, sparsely to densely pubescent to villous, beset with glandular hairs, green but turning brown with age. *Leaves* crowded at ends of branches, alternate, simple, petiolate; lamina (20–)

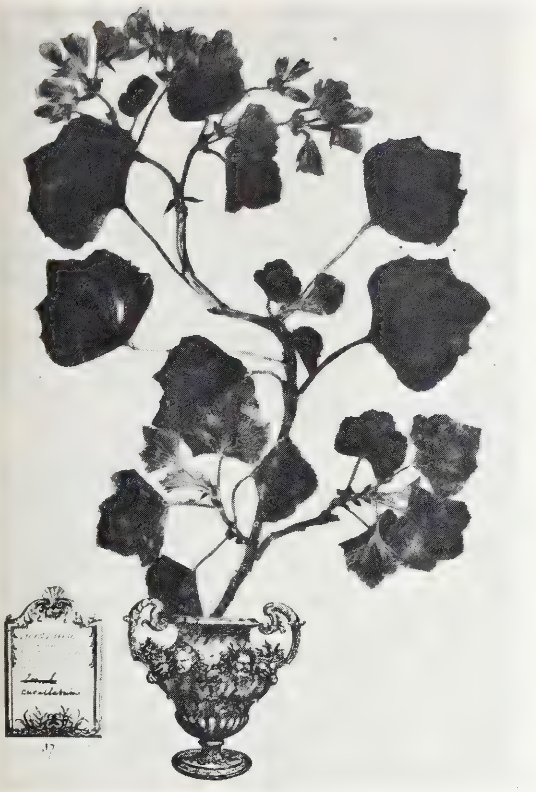

FIG. 2.—*Pelargonium cucullatum* (L.) L'Hérit. subsp. *cucullatum*. Lectotype: specimen in Hort. Cliff. 345.17 of *Geranium cucullatum* L. in BM. Photo: J.J.A. van der Walt.

40–55 (–110) mm long and (20–) 50–90 (–180) mm wide, firm, flat to hood-shaped at base, circular, reniform or triangular in outline, with or without shallow angular incisions, base reniform, cordate, obtusely subcordate or cuneately incised, margin irregularly denticulate, often entire in proximal ¼ of lamina, margin occasionally red, strigose or villous, beset with glandular hairs, veins adaxially sunken below leaf surface but abaxially prominent, green; petiole (8–) 20–55 (–90) mm long, subcylindrical, somewhat flattened dorsiventrally, adaxially grooved, villous and beset with glandular hairs, stipules 5–10 mm long and 3–7 mm wide, free, ovate to narrowly ovate with acute apices, membranous, densely pilose, caducous, light green. *Inflorescence* a branched flowering stem bearing up to 4 pseudo-umbels of (1–) 3–9 (–13) flowers each, with 1–2 small foliar leaves and 2–4 bracts at each ramification; bracts 5–9 mm long and 2–4 mm wide, ovate to broadly ovate with acute apices, sparsely pilose to villous (especially abaxially and at margins), green; peduncle (20–) 30–60 (–70) mm long, erect, sometimes slightly bent in bud stage, becoming nodding-recurved after flowering, pubescent or polose, beset with glandular hairs, green or tinged with red. *Pedicel* 2–7 (–11) mm long, villous, green or reddish brown. *Hypanthium* 5–12 mm long, villous, green or reddish brown. *Sepals* 5, 12–20 mm long and 2–6 mm wide, elliptic to narrowly elliptic with acute apices, villous (indumentum abaxially longer than adaxially), green or reddish brown. *Petals* 5, 15–32 mm long and 6–17 mm wide, light pink or dark pinkish purple, rarely white; posterior two obovate, asymmetric, with dark purple streaks and a reddish purple tinge at the bases widening to reddish purple patches; three anterior petals 15–28 mm long and 6–12 mm wide, obovate to elliptic to narrowly elliptic, with reddish purple markings. *Stamens*: 7 fertile (rarely less) [two 12–18 (15) mm, two 10–16(13) mm, two 8–13(9) mm and one 11–15 (12) mm long]; staminodes 3 (rarely more), 5–10 (8) mm long; staminal column white to pale pink; anthers 2–3 mm long, dorsifixed, introrse, purple; pollen orange. *Gynoecium*: style reddish purple, 6–9 mm long, proximal half sparsely pilose; stigmata 5, 2–4 mm long, dark reddish purple. *Mericarps* 15–31 mm long (base 4–6 mm long, tail 11–25 mm long). *Seed* 3–4 mm long.

KEY TO THE SUBSPECIES

Margin of lamina more or less angularly incised:
  Lamina villous; central vascular bundle in petiole with a fibrous column .... (a) subsp. *cucullatum*
  Lamina strigose; central vascular bundle in petiole mostly without a fibrous column ...... (c) subsp. *strigifolium*
Margin of lamina not angularly incised, lamina villous; central vascular bundle in petiole with a fibrous column .... (b) subsp. *tabulare*

(a) subsp. **cucullatum**

Geranium cucullatum L., Sp. Pl. edn 1: 677 (1753) pro parte, emend. Volschenk; Burm. f., Geran. 35 (1759) pro parte; L., Sp. Pl. edn 2: 946 (1763) pro parte; Berg., Descr. Pl. Cap. 174 (1767) pro parte; Burm. f., Prodr. Fl. Cap. 18 (1768) pro parte; Thunb., Prodr. 114 (1794) pro parte; Fl. Cap. 518 (1823) pro parte — var. *fimbriatum* Burm. f., Geran. 35 (1759); Prodr. Fl. Cap. 18 (1768). *Pelargonium cucullatum* (L.) L'Hérit. in Ait., Hort. Kew edn 1, 2: 426 (1789) pro parte; Van der Walt, Pelargoniums S. Afr. 1: 12 (1977) pro parte; Van der Walt & Vorster, Pelargoniums S. Afr. 2:43 (1981) *Geraniospermum cucullatum* (L.) Kuntze, Rev. Gen. 1: 93 (1891).

Geranium angulosum Mill., Gard. Dict. edn 8: no. 22 (1768). *Pelargonium angulosum* (Mill.) L'Hérit. in Ait., Hort. Kew. edn 1, 2: 426 (1789); Salisb., Prodr. 314 (1796); Willd., Sp. Pl. 3: 671 (1800); Pers., Syn. Pl. 2: 231 (1807); Willd., Enum. 706 (1809); Ait. f., Hort. Kew edn 2, 4: 174 (1812); DC., Prodr. 1: 672 (1824); G. Don, Gen. Syst. 1: 740 (1831); Eckl. & Zeyh., Enum. 1: 80 (1835); Harv. in Fl. Cap. 1: 302 (1860); Knuth in Pflanzenreich 4, 129: 460 (1912); Salter in Adamson & Salter, Fl. Cape Penins. 518 (1950). *Geraniospermum angulosum* (Mill.) Kuntze, Rev. Gen. 1: 94 (1891).

Geranium acerifolium Cav., Diss. 4: 243, t. 112, fig. 2 (1787); Thunb., Prodr. 114 (1794); Fl. Cap. edn 2: 520 (1823). Iconotype: Cav., Diss. 4: t. 112, fig. 2 (1787).

Diagnostic features

Lamina sightly to strongly hood-shaped, shallowly and angularly incised in distal half, base obtusely subcordately to cuneately incised, villous; *petiole* usually shorter than lamina, with a central fibrous column present in the central vascular bundle. *Pseudo-umbels* with 5–7 flowers each. *Petals* usually dark pinkish purple, occasionally white. (Fig. 3).

Geographical distribution and habitat

The subsp. *cucullatum* has a small, continuous distribution from the vicinity of Gansbaai in the east to Gordon's Bay in the west, with a few isolated populations in the Cape Peninsula which are separated from the rest by False Bay. The leaves of the plants on the peninsula are less villous than

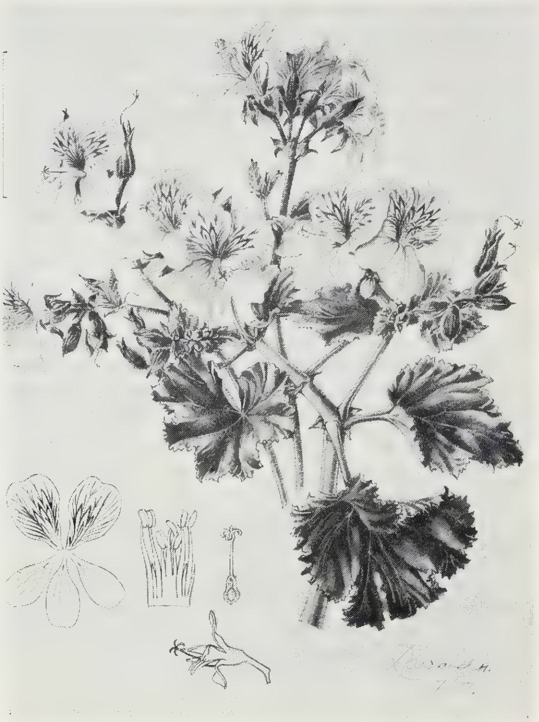

FIG. 3.—*Pelargonium cucullatum* (L.) L'Hérit. subsp. *cucullatum*. Scale denotes 50 mm.

elsewhere. The plants occur from near the high water mark on the narrow coastal flats and in the lower foothills of the mountains, but always practically within sight of the sea (Fig. 1).

The subsp. *cucullatum* is a constituent of moist coastal fynbos. It occurs under rainfall regime of 400–800 mm per annum, on well-drained, sandy soils which are mainly derived from Table Mountain Sandstone.

Flowering takes place from September to February. The impression was gained that individual plants of this subspecies have a longer flowering period than the subsp. *tabulare*, and this may be ascribed to the moister, perhaps more favourable environmental conditions experienced by the subsp. *cucullatum*.

Material studied

CAPE.—3318 (Cape Town): Table Mountain, near Constantia (–CD), *Ecklon 623* (W). 3418 (Simonstown): Kalkbaai (–AB), *Zeyher s.n. in SAM 14592* (SAM); Muizenberg (–AB), *Dümmer 512* (E); *Lansdell s.n. in PRE 55718* (PRE); *MacOwan 79* (BOL; PRE; SAM; W); *Marloth 35* (PRE); *Penther 2171* (W); *Scott-Elliot 197* (E); Silver Mine Valley (–AB), *Pillans 2708* (BOL); Simonstown (–AB), *Marloth 3615* (PRE; STE); *Volschenk 22* (STE-U); Gordon's Bay (–BB), *Davis s.n. in SAM 66648* (SAM); *Duthie 306* (STE-U); *Volschenk 40* (STE-U); between Gordon's Bay and Betty's Bay (–BD), *Dyer 5761* (PRE); between Gordon's Bay and Koëlbaai (–BD), *Ihlenfeldt 1673* (PRE); Betty's Bay (–BD), *Rycroft 2722* (NBG); *2775* (NBG); *3155* (NBG); *Van der Schijff 7424* (PRE); *Van der Walt 433* (STE-U); *Volschenk 23* (STE-U); *49* (STE-U); *Werdermann & Oberdieck 711* (PRE); Hangklip (–BD), *Rodin 3126* (BOL); *Taylor 5866* (NBG); Harold Porter Reserve (–BD), *Ebersohn 62/68* (NBG); *Van der Walt 649* (STE-U); Koëlbaai (–BD), *Boucher 473* (PRE). 3419 (Caledon): near Hermanus (–AC), *Gillett 28* (STE); *Jordaan 896* (STE); *Rogers 26600* (PRE); *Van der Walt 492* (STE-U); Kleinmond (–AC), *Pillans 8234* (BOL); Strey *2964* (PRE); *Van Breda 1432* (PRE); *Volschenk 1* (STE-U); *2* (STE-U); *3* (STE-U); *4* (STE-U); Voëlklip (–AC), *Barker 1613* (NBG); Kleinrivier Mountains (–AD), *Ecklon 625* (W); Mosselrivier (–AD), *Potts 5011* (SAM); *Verkiis s.n. in STE 11215* (STE); near Stanford (–AD), *Radloff s.n. in STE-U (ser. 1) 13696* (PRE); between Stanford and Hermanus (–AD), *Gillett 4175* (BOL); *Marsh 872* (STE).

Taxonomic notes

Our interpretation of Linnaeus's concept of *Geranium cucullatum* is based on the following sources which were available from the original description in L., Sp. Pl. edn 1: 677 (1753):

1. Linnaeus's description (GERANIUM calycibus monophyllis, foliis cucullatis dentatis). This is insufficient to distinguish from one another the three subspecies recognized in the present treatment.

2. Specimens seen by Linnaeus: the only specimens which had definitely been seen by Linnaeus before the publication of the Species Plantarum, are two sheets in the Clifford Herbarium in BM, almost certainly the subject(s) of Linnaeus's Hort. Cliff. 345 (1738) (see below). Both have the trivial name *cucullatum* written in Linnaeus's own handwriting. We have chosen the first of these, no. 345.17, as a lectotype specimen of *Geranium cucullatum,* because it reflects the major part of Linnaeus's concept as evidenced by the literature citations discussed below. The second specimen, no. 345.17∝, represents a different taxon and is taken as basis for the subsp. *tabulare* Volschenk as distinguished in the present work.

3. Linnaeus's reference to previous publications:

a. Linnaeus, Hort. Cliff. 345 (1738): the description is practically identical to that in Sp. P1. *l.c.* In addition Linnaeus cited from Boerhave, Lugdb. 263 (1720) '. . . folio hirsuto . . .'

b. Dillenius, Hort. Elth. 155, t. 129, fig. 156 (1732): the description 'foliis . . . minus angulosis, . . . mollitiem', as well as the illustration, clearly concern the subsp. *cucullatum.*

c. Hermann, Hort. Lugdb. Bat. 274 (1687): the illustration on p. 275 is of the currently recognized subsp. *cucullatum.*

d. Martyn, Hist. Pl. Rar. Cent. 28, t. 28 (1728): the description 'folia . . . sinuata seu potius angulosa . . . utrinque villosa' as well as the accompanying illustration clearly concern the subsp. *cucullatum.*

e. Van Royen, Lugdb. 353 (1740): described it as 'folio hirsuto cum fimbriis purpureis'. In addition Van Royen cited Linnaeus's Hort. Cliff. *l.c.*, which, as we have seen above, appears to comprise two elements.

f. Linnaeus, Hort. Ups. 196 (?): not seen.

Wendland (Coll. Pl. 3, 45: t. 54 (1806)) described *P. rubens* from the Cape. From his description and figure it seems to be synonymous with *P. cucullatum* subsp. *cucullatum*, but in the absence of a specimen there cannot be absolute certainty.

(b) subsp. **tabulare** *Volschenk,* subsp. nov., a subsp. *cucullato* lamina circulari basi reniformi vel cordata; a subsp. *strigifolio* lamina villosa non strigosa margine non angulari basi non cuneata, petalis e atro-subroseis purpureis non pallide roseis vel e subroseis purpureis differt.

Type: Africa, without precise locality, specimen in Hort. Cliff. 345. 17 (BM, holo!). Figs. 4 & 5.

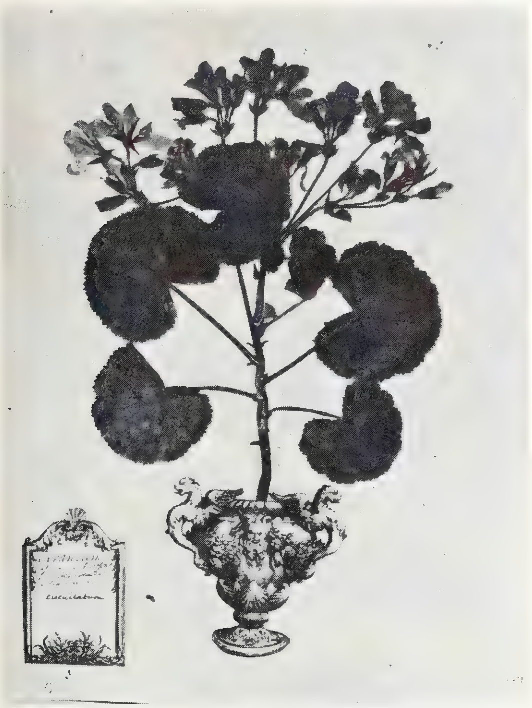

FIG. 4.—*Pelargonium cucullatum* (L.) L'Hérit. subsp. *tabulare* Volschenk. Lectotype: specimen in Hort. Cliff. 345.17∝ in BM. Photo: J.J.A. van der Walt.

Geranium cucullatum L., Sp. Pl. edn 1: 677 (1753) pro parte; Burm. f., Geran. 35 (1759) pro parte; L., Sp. P1. edn 2: 946 (1763) pro parte; Berg., Descr. P1. Cap. 174 (1767) pro parte; Burm. f., Prodr. F1. Cap. 18 (1768) pro parte; Cav., Diss. 4: 241, t. 106, fig. 1 (1787); Thunb., Prodr. 114 (1794) pro parte; F1. Cap. 518 (1823) pro parte. *Pelargonium cucullatum* (L.) L'Hérit. in Ait., Hort. Kew ed. 1, 2: 426 (1789) pro parte; Willd. Sp. P1. 3: 670 (1800); Enum. 706 (1809); Pers., Syn. P1. 2: 231 (1807); Ait. f., Hort. Kew. edn 2, 4: 174 (1812); DC., Prodr. 1: 671 (1824); Spreng., Syst. Veg. 3: 58 (1826); G. Don, Gen. Syst. 1: 740 (1831); Eckl. & Zeyh., Enum. 1: 80 (1835); Harv. in Fl. Cap. 1: 302 (1860); Marloth, F1. Kapl. 116, fig. 30 (1908); Knuth in Pflanzenreich 4, 129: 466 (1912); Marloth, F1. S. Afr. 2: 90 (1925); Salter in Adamson & Salter, F1. Cape Penins. 518 (1950); Mason, Western Cape Sandveld Flow. 134, t. 56 (1972); Van der Walt, Pelargoniums S. Afr. 1: 12 (1977) pro parte (pro icon.).

Diagnostic features

Lamina hood-shaped, circular in outline, base reniformly to cordately incised, villous; *petiole* equalling or exceeding lamina in length, with a central fibrous column present in the central vascular bundle. *Pseudo-umbels* with (5–) 6–9 (–13) flowers each. *Petals* usually dark pinkish purple. Fig. 5.

Geographical distribution and habitat

The subsp. *tabulare* occurs in two relatively restricted areas separated from each other by a distance of about 90 km; namely on the Cape Peninsula where it ranges from Lion's Head and Table Mountain southwards to Cape Point, and in the vicinity of Saldanha Bay (Fig. 1). On the Cape Peninsula it occurs as a component of fynbos, from sea level to about 500 m against the mountain slopes, but always practically within sight of the sea. It grows on well-drained, usually stony and often sandy soils derived from Table Mountain Sandstone, shale and tillite. It receives an annual rainfall of 400–1 000 mm on the Cape Peninsula. In the Saldanha Bay area it occurs in fynbos vegetation in sheltered ravines, under conditions somewhat reminiscent of those on the Cape Peninsula, but receiving only about 200 mm of rain per annum.

It should be noted that the Saldanha Bay plants are smaller than those on the Cape Peninsula, especially in respect of the leaves and flowers, but this appears to be a result of less favourable environmental conditions and is not of taxonomic significance.

The flowering period stretches from late September to February, with a peak in October and November.

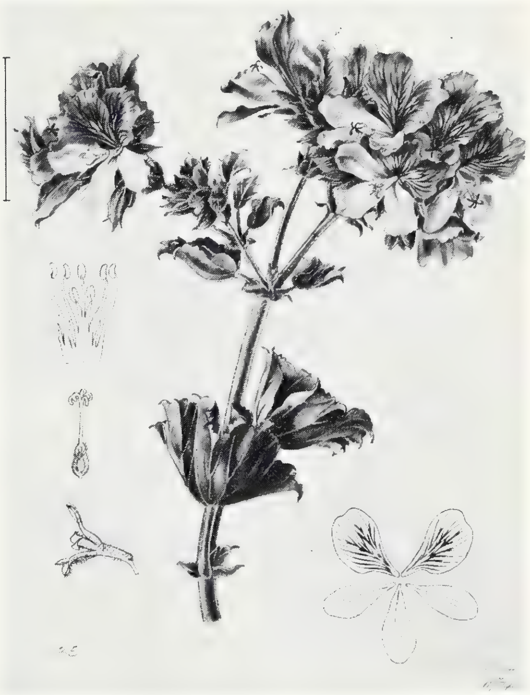

FIG. 5.—*Pelargonium cucullatum* (L.) L.'Hérit subsp. *tabulare* Volschenk. Scale denotes 50 mm.

Material studied

CAPE.—3318 (Cape Town): Langebaan (–AA), *Axelson 3576* (NBG); *Taylor 3773* (NBG); Postberg Nature Reserve (–AA), *Volschenk 28* (STE-U); *29* (STE-U); peninsula west of Saldanha Bay (–AA), *Pillans 6883* (BOL); *Salter 3925* (BOL); Camp's Bay (–CD), *Ecklon & Zeyher 4827* (SAM); *Marloth 9356* (PRE); *Volschenk 9* (STE-U); *10* (STE-U); Cape Town (–CD), *Pegler s.n. in PRE 55751* (PRE); *Young s.n. in PRE 26417* (PRE); Devil's Peak (–CD), *Thompson 31* (PRE); *Wolley-Dod 2469* (BOL); Kirstenbosch (–CD), *Grant 2639* (PRE); north of Window Stream (–CD), *Esterhuysen 501* (BOL; PRE); Lion's Head (–CD), *Van der Walt 470* (STE-U); Sea Point (–CD), *Willms 3074* (Z); Signal Hill (−CD), *Volschenk 6* (STE-U); 7 (STE-U); *8* (STE-U) Table Mountain (−CD), *Bolus 2729* (BOL); *Dümmer 332* (E); *Ecklon 608* (W)*; *Ecklon & Zeyher 621* (SAM; W); *Flanagan 2415* (PRE); *Guthrie 2394* (NBG; PRE); *MacOwan 6472* (SAM); *Rodin 3221* (BOL; PRE); *Schenk 551* (Z); *Thode A5* (PRE); *Werdermann & Oberdieck 65* (PRE). 3418 (Simonstown): farm Bergvliet (−AB), *Purcell 237* (SAM); *s.n. in BOL 16377* (BOL); south of Houtbaai (−AB), *Smuts s.n.* (STE); Muizenberg (−AB), *Pillans s.n. in PRE 16366* (PRE); Oceanview near Kommetjie (−AB), *Van der Walt 664* (STE-U); Simonstown, Red Hill (−AB), *Leighton 3062* (BOL); *Pillans 2194* (BOL); *Rogers 11282* (PRE); Wynberg Hill (−AB), *Salter 6393B* (BOL); *Verdoorn s.n. in PRE 55752 (PRE);* Cape of Good Hope Nature Reserve (−AD), *Dahlstrand 1080* (PRE); Cape Point (−AD), *Herre s.n. in STE 11745* (STE); Buffelsbaai (−AD), *Gillett 768* (STE); Olifantsbos (−AD), *Leighton 3055* (BOL); *3056* (BOL); *3057* (BOL); *Rycroft 2189* (NBG); near Vasco da Gama Hill (−AD), *Hutchinson 652* (BOL; PRE).

(c) subsp. **strigifolium** *Volschenk*, stat. et nom. nov. Type: as for *P. acerifolium* L'Hérit. below.

Pelargonium acerifolium L'Hérit. in Ait., Hort. Kew. edn 1, 2: 427 (1789); Geran. t. 21 (1792); Salisb., Prodr. 315 (1796); Pers., Syn. P1. 2: 231 (1807); Willd., Enum. 706 (1809); Ait. f., Hort. Kew. edn 2, 4: 174 (1812); DC., Prodr. 1: 672 (1824); Spreng., Syst. Veg. 3; 61 (1826); Eckl. & Zeyh., Enum. 1: 80 (1835); Knuth in Pflanzenreich 4, 129: 461 (1912); non *Geranium acerifolium* Cav. (1787). *Pelargonium angulosum (Mill.)* L'Hérit. var. *acerifolium* (L'Hérit.) Harv. in Fl. Cap. 1: 303 (1860) Iconotype: L'Hérit., Geran. t.21 (1792). Fig 6.

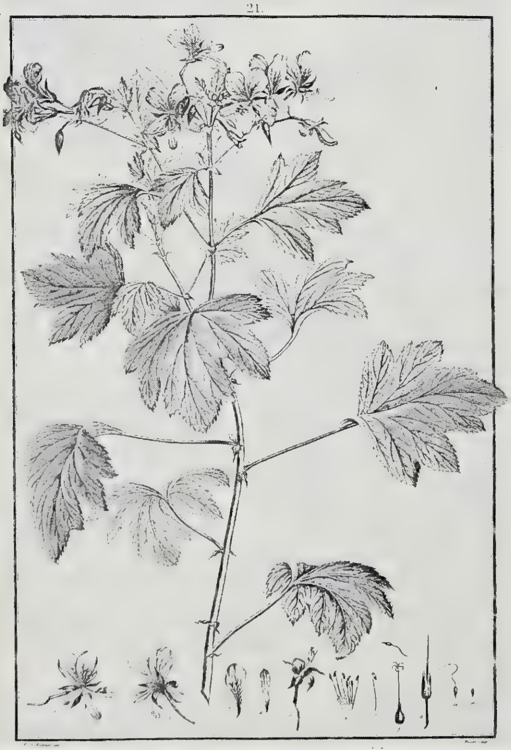

FIG. 6.—*Pelargonium cucullatum* (L.) L'Hérit. subsp. *strigifolium* Volschenk. Iconotype: L'Hérit. Geran. t. 21 (1792).

Diagnostic features

Lamina flat to somewhat hood-shaped, shallowly and angularly incised in distal half, base cuneately incised, strigose and with glandular hairs longer than ordinary hairs; *petiole* usually shorter than lamina, with a central fibrous column absent (rarely present) in the central vascular bundle. *Pseudo-umbels* with 3−5 flowers each. *Petals* usually light pink to pinkish purple. Fig. 7.

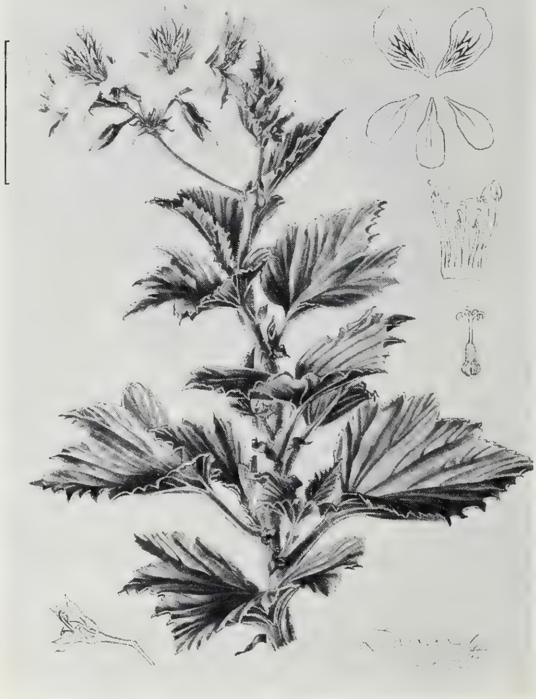

FIG. 7.—*Pelargonium cucullatum* (L.) L'Hérit. subsp. *strigifolium* Volschenk. *Drijfhout* 436 from the farm La Motte near Franschhoek, flowering under glass in Stellenbosch. Scale denotes 50 mm.

Geographical distribution and habitat

The subsp. *strigifolium* has a montane distribution in the south-western Cape Province, being known from the mountains around Bainskloof in the north to Baardskeerdersbos in the south, and the southern Hottentotsholland Mountains in the west to the Kleinrivier Mountains near Caledon in the east, at altitudes of 300−900 m. In contrast to the subspecies *cucullatum* and *tabulare,* this subspecies does not occur in close proximity to the sea.

Like the other two subspecies, it is a constituent of fynbos. Few precise rainfall figures are available for its montane habitats, but the rainfall over the general area varies from about 600 to 1 000 mm per annum. It grows on soils derived from sandstone, shale and tillite, and in the vicinity of Paarl and Jonkershoek also on soils derived from granite and granofir. These soils can be quite heavy.

Plants from the Swartberg near Caledon are smaller than elsewhere, probably occurring under less than optimal conditions at the eastern border of

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[*] Ecklon & Zeyher 608 is the type of *Eumorpha catarractae* Eckl. & Zeyh., Enum. 1: 78 (1835). Specimens in S! and SAM! match *Pelargonium patulum* Jacq.

the area which is climatically suitable for this subspecies.

Flowering takes place from September to January, with a peak in October and November.

Material studied

Cape.—3318 (Cape Town): Paarl Mountain (−DB), *Marais s.n. in STE-U 1742* (STE-U); *Marloth 3480* (PRE); *Van der Walt 652* (STE-U); *Volschenk 12* (STE-U); *33* (STE-U); Wellington (−DB), *Knobel s.n. in PRE 23760* (PRE); Jonkershoek (−DD), *Borchardt 301* (STE); *Marais s.n. in STE-U 1030* (STE-U); *Smith 306b* (STE-U); *Van der Walt 428* (STE-U); *506* (STE-U); *641* (STE-U); *Volschenk* (STE-U); 5 Jonkershoek, Assegaaiboskloof (−DD), *Van der Walt 517* (STE-U); Jakkalsvlei (−DD), *Taylor 5153* (STE); *6956* (PRE); Swartboskloof (−DD), *Van der Merwe 2126* (STE); *Van der Walt 418* (STE-U); *Van Rensburg 2074* (PRE); *Walgate 987* (STE); Stellenbosch (−DD), *Wawra 123* (W); Stellenbosch, Botmaskop (−DD), *Van der Walt 537* (STE-U); *Van Rensburg 371* (STE); *374* (STE); near Paradise (−DD), *Herre s.n. in STE 306a* (STE); *306b* (STE). 3319 (Worcester): Bainskloof (−CA), *Gillett 788* (BOL); *Kies 43* (NBG); Du Toitskloof, western entrance (−CC), *Pillans 8461* (BOL); Franschhoek (−CC), *Boucher 2353* (PRE; STE); *Phillips 1058* (SAM); *R.G. 5136* (PRE); *Thode A2187* (PRE); *Volschenk 35* (STE-U); Franschhoek Forest Reserve (−CC), *Esterhuysen s.n.* (BOL); Klein Drakenstein Mountains, Kasteelkloof (−CC), *Kruger 1465* (STE); mountains between Franschhoek and Villiersdorp (−CC), *Bolus 5136* (BOL); Wemmershoek Mountains (−CC), *Drijfhout 463* (STE-U); *Esterhuysen 4044* (PRE); *17718* (BOL; PRE). 3418 (Simonstown): mountains south of Gordon's Bay (−BB), *Marloth 10119* (PRE); *Smith 306a* (STE-U); Hottentotshollandkloof (−BB), *Ecklon & Zeyher 627* (SAM: W); Koëlberg Forest Reserve (−BB), *Rycroft 1438* (BOL; NBG; PRE); Sir Lowry's Pass (−BB), *Volschenk 39* (STE-U); Steenbras Dam (−BB), *de la Bat s.n. in STE-U 108* (STE; STE-U); *Salter 6518* (BOL); Arieskraal near Palmiet River (−BD), *Barker 3335* (NBG); *Leighton 784* (BOL); between Betty's Bay and Cape Hangklip (−BD), *Ihlenfeldt 1718* (PRE); Kleinmond (−BD), *Compton 12370* (NBG). 3419 (Caledon): between Villiersdorp and Elgin (−AA), *Bayliss 707* (PRE); Elgin (−AA), *Van Breda 563* (PRE); Grabouw (−AA), *Bolus 4112b* (BOL); *4112c* (BOL); Lebanon River (−AA), *Van der Zel Z19* (PRE); *Z65* (PRE); Houhoek Pass, 5 km west of Botrivier (−AA), *Barker 8804* (NBG); *Volschenk 38* (STE-U); Palmiet River (−AA), *Penther 2153* (W); Caledon (−AB), *Penther 2136* (W); Swartberg (−AB), *Galpin 3820* (PRE); *Volschenk 36* (STE-U); *Zeyher s.n. in PRE 55753* (PRE); *in SAM 13633* (SAM); *in SAM 14593* (SAM); Paardeberg at Palmiet River Mouth (−AC), *Grobler 29286* (PRE; STE); Caledon, Hartebees River (−BC), *Elbrecht 22136* (PRE); near Strandkloof (−CB), *Van der Walt 603* (STE-U); Baardskeerdersbos, on the hills (−DA), *Volschenk 44* (STE-U).

Taxonomic notes

We chose a completely new epithet for this subspecies, to avoid possible future confusion between the names *Pelargonium acerifolium* L'Hérit. (which is superseded by the new name *P. cucullatum* subsp. *strigifolium)* and *Geranium acerifolium* Cav. Although this does not preserve continuity of epithet, it is permissible under Article 11.3 (ICBN, 1978), which states that an epithet has priority only within its own rank.

Pelargonium acerifolium L'Hérit. (1789) is not considered to be a recombination based on *Geranium acerifolium* Cav. (1787), but rather as a different name, because L'Héritier made no direct or indirect reference to Cavanilles and actually was concerned with a different taxon.

ACKNOWLEDGEMENTS

We would like to express our appreciation to the following: the C.S.I.R. and the Research Fund of the Univerity of Stellenbosch, for financing the research project on Geraniaceae; Dr D. J. B. Killick and Mr C. H. Stirton of the Botanical Research Institute in Pretoria for valued advice regarding matters of typification; Mrs E. Ward-Hilhorst for preparing the accompanying paintings of the plants; the Directors and Curators of the various herbariums who kindly loaned to us their herbarium material of this complex, as indicated in the inventories of specimens studied.

UITTREKSEL

Dit word aangetoon dat Pelargonium cucullatum *(L.) L'Hérit. bestaan uit drie infraspesifieke taksons waaraan subspesifieke rang toegeken word onder die name* P. cucullatum *subsp.* cucullatum, *subsp.* **tabulare** *Volschenk en subsp.* **strigifolium** *Volschenk. Dit is verder bewys dat* P. angulosum *(Mill.) L'Hérit.* (Geranium angulosum *Mill.*) *sinoniem is met* P. cucullatum *subsp.* cucullatum, *maar dat die naam* P. angulosum *vir baie jare verkeerdelik op subsp.* strigifolium *toegepas is. Laasgenoemde was vroeër bekend as* P. acerifolium *L'Hérit., non* Geranium acerifolium Cav.

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Bothalia 14, 1: 53–67 (1982)

Taxonomic status of the endemic South African bamboo, *Thamnocalamus tessellatus*

THOMAS R. SODERSTROM* and R. P. ELLIS**

ABSTRACT

Thamnocalamus **tessellatus** (Nees) Soderstrom & Ellis, comb. nov. [= *Arundinaria tessellata* (Nees) Munro] is the only endemic South African bamboo and occurs from the eastern districts of the Cape, through Lesotho and Natal, to the eastern Orange Free State at elevations of about 1 500–2 500 m. The Mountain Bamboo, or 'Bergbamboes' was first described by Nees in 1841 as a member of the genus *Nastus* because of the similarity, to him, of the spikelets between it and *N. borbonicus,* but was later transferred to the all-encompassing genus of the time, *Arundinaria,* the type species of which is endemic to the south-eastern United States of America. Based on our present knowledge of bamboo genera, this South African species may be excluded from *Nastus* because the inflorescence is not a panicle but bracteate racemiform, the vegetative branches do not arise in a verticillate manner but are a series of subequal branches that are borne in a row above the nodal line and *T. tessellatus* has an androecium of three stamens and not six as in *Nastus.* The Bergbamboes, with sympodial rhizomes and branch complement of several subequal branches, can also not be maintained in *Arundinaria,* for monopodial rhizomes and a single branch at the node are typical of this genus. The simple, ebracteate, and exserted inflorescence of *Arundinaria* is also quite distinct from that of the Bergbamboes.

In order to place the South African bamboo more precisely we have made comparative studies of its leaf anatomy and epidermis, gross morphology, and analyses of its inflorescence and spikelets. The results of all these studies reveal a striking resemblance to members of the Sino-Himalayan genus, *Thamnocalamus,* to which we have accordingly transferred the species. The results are presented, together with an interpretation of the phylogenetic position of the Bergbamboes and possible events that led to the disjunction of species in the genus.

INTRODUCTION

The Republic of South Africa has but a single endemic bamboo, commonly known as the 'Bergbamboes'. The cresent-shaped distribution range of this tree grass is marked in the south-west by the 'Bamboesberg', west of Tarkastad, and in the north-east by Van Reenen's Pass in the Drakensberg, the bamboo occurring in the mountains between both points as they pass from the Cape through Lesotho and into the Orange Free State and Natal. The Bergbamboes, whose smooth narrow culms may reach 5 metres, produces clusters of branches with stiff foliage from the upper nodes giving them the appearance of gigantic plumes. The plants prefer stream edges and produce roots with air canals that verify this adaptation for wet conditions. As is a common phenomenon in most bamboos, the plants remain vegetative for many years and spread by means of rhizomes, producing flowers and fruits only rarely.

The earliest collections were sterile gatherings, and Nees von Esenbeck named the bamboo as a species of *Nastus* in his grass treatment for the 'Florae Africae Australioris' (1841). His studies were made on collections of Ecklon and Drège from various mountains in the Cape and in these he noted a similarity to *Nastus borbonicus* J. E. Gmel., perhaps in the tessellate (?) foliage and clusters of subequal branches at the nodes, which are common to both. Munro (1868), in his treatment of bamboos of the world, transferred the species to the genus *Arundinaria,* remarking that he had no authority to do so except for the great resemblance it bore in habit and general appearance to that genus, especially *A. macrosperma* Michx. (now considered a synonym of *A. gigantea* Michx., type of the genus).

The type species of *Arundinaria* is the only bamboo native to the United States and occurs principally in the south-eastern part of the country where it is called 'Canebrake'. Michaux (1903) described the bamboo as *Arundinaria gigantea* in his 'Flora Boreali-Americana', and since that time the genus has become a repository for innumerable kinds of bamboos from throughout the world. Munro's inclusion of the Bergbamboes in this genus was not at all unusual; his opinion was later supported by the agrostologist at Kew, Sir Otto Stapf, who wrote a detailed account of the bamboo in 1900. He pointed out the real need for flowering material.

Stapf's desire was soon fulfilled for in 1908 Mrs W. Putterill discovered flowering plants in the Drakensberg, near Harrismith, and sent specimens of these to Kew. Stapf (1909) immediately published a description of the flowering material, maintaining the species in *Arundinaria,* but noting its particular resemblance to the Himalayan species, *A. spathiflora* Trin. Stapf felt, however, that the 2-flowered spikelets (they are actually 4-flowered) and nature of the glumes (?) ruled out such an alliance.

The Bergbamboes has been maintained in *Arundinaria* since the time of Munro and its placement not questioned since Stapf. The late bamboo specialist, F. A. McClure, presented a detailed description and analysis of the type species of *Arundinaria* in his treatment of bamboo genera native to the New World (1973). For the New World alone, 53 species had been assigned to the genus and McClure allocated these among nine genera, showing how all-inclusive and heterogenous the

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genus had become. Although he did not treat the Old World species, McClure's unpublished notes indicate that he also did not regard the Bergbamboes as a member of *Arundinaria* but rather of *Thamnocalamus,* a Himalayan genus based on *Arundinaria spathiflora.*

In view of the different opinions concerning the taxonomic position of the Bergbamboes, we have made comparative studies of its leaf anatomy and epidermis and gross morphology, along with an analysis of the inflorescence and spikelets. Our studies confirm the suggestion by Stapf that a relationship does occur with *'Arundinaria' spathiflora.* We agree with McClure, who recognized Munro's genus *Thamnocalamus* (based on that species) and who felt that the Bergbamboes belonged there as well.

SYNOPSIS

Thamnocalamus tessellatus *(Nees) Soderstrom & Ellis,* comb. nov. Lectotype: Cape, 'in monte Katberg, alt. 500′ ', *Drège* s.n. (K; PRE, fragment ex K).

Nastus tesselatus Nees von Esenbeck. Florae Africae Australioris, 463 (1841). Syntypes: Cape, 'In monte Winterberg alt. VI. (Terrae Caffrorum), *"Ecklon* s.n."; in praeruptis udis montium Witbergen alt. 5000–6500′ vulgatissima, etiam in monte Los-Tafelberg 'in den Kränzen' eadem altitudine, in Bambbusergen aliisque in locis editissimis circa fines Caffrorum, tum vero et in monte Katberg alt. 500′,' *Drège s.n.* (K; PRE fragment ex K).

Arundinaria tessellata (Nees) Munro. Monograph of the Bambusaceae, Trans. Linn. Soc. Bot. 26: 31. (1868); non Bean, Gdnrs' Chron. ser. 3, 15: 338 (1899).

In his original description of *Nastus tessellatus,* Nees listed specimens collected by Ecklon and Drège on various mountains in the Cape. We have chosen as the lectotype the collection of Drège on the Katberg, of which there is a fragment at PRE from the complete specimen at K.

MORPHOLOGICAL DESCRIPTION

Loosely tufted bamboo with hollow culms 1–5 m tall, 2 cm in diameter, erect or only slightly arching, dark maroon when young, becoming stramineous, waxy with age, the branches confined to the upper nodes and producing a plumelike effect. *Rhizomes* sympodial with necks 25–30 cm long and thick roots containing air canals. *Nodes* not thickened, containing a single bud. *Culm leaves* somewhat persistent: sheath pale maroon with fine pencil-thin stripes when young; blade persistent, at first ascending, becoming horizontal-concave. *Branching* intravaginal, occurring at the upper nodes of the culm, consisting of several (5–8) subequal branches above the nodal line, these rebranching and resulting in 10–12 branches that form dense tufts of foliage at the node, the branches 10–30 cm long. *Foliage leaves:* leaf complement of 3–5 closely overlapping leaves with blades up to 15 cm long and 1–1,5 cm wide on the primary branches, 5–6 cm long and up to 0,8 cm long on the branches of further orders, the blades stiff, narrowly lanceolate, gradually tapering below to a petiole 1–2 mm long and to an acuminate, navicular apex forming a hard point, the midrib prominent on the lower surface with 3 or 4 pairs of secondary nerves, the margins cartilaginous and antrorsely scabrous, both surfaces otherwise smooth, sometimes pubescent toward the base of the blade, especially on one side of the midnerve, the tessellation generally manifest on both surfaces; ligule a truncate membrane up to 1,5 mm long, glabrous except for a few cilia on the upper margin; sheath strongly ribbed, glabrous on the back, the upper margin consisting of a short-ciliolate collar and ciliate margins on either side of the petiole.

Inflorescence terminating the branches, the uppermost nodes of which bear long sheaths (their small blades caducous) that exceed the length of the inflorescence, these sheaths strongly overlapping, becoming stramineous and frayed with age; inflorescence consisting of 3–5 spikelets, the lowermost sessile and subtended by a bract, the succeeding spikelets preceding the terminal one each with a short pedicel, the whole unit (including the bracts) c. 4 cm long; subtending bracts glabrous, strongly ribbed, becoming incurved, truncate at the apex; axis of the inflorescence thick, angular, short-hispid with a few longer hairs at the nodes and on the angles; subtending bracts on the axis present below the lowest spikelet and sometimes at a higher node, white, many-nerved, glabrous, with an acute tip.

Spikelets more or less ovoid, 15,4–17,4 mm long, 4-flowered, the lower two florets most fully developed with the second slightly elevated above the first but a little smaller in size, the third depauperate and consisting of a small lemma enclosing a tiny rudimentary palea and flower, the fourth quite rudimentary; glumes 2, glabrous, the lower a little shorter than the upper, broad at the base and narrowing to an acute tip; glume 1 lanceolate from the side, 9,9–11,5 mm long, 8- or 9-nerved with a few transverse veinlets, glabrous; glume 2 lanceolate from the side, pointed, 14,0–15,0 mm long, 9–13 nerved with transverse veinlets, glabrous; lemma oblong-lanceolate from the side, 11,1–15,0 mm long, 10- or 11-nerved with transverse veinlets, minutely ciliolate on the upper margins, otherwise glabrous; palea broadly lanceolate in side view, 10,0–12,5 mm long, 2-keeled with a sulcus between the keels and shortly bifid at the summit between them, with 2 broad wings, faintly 2- or 3-nerved between the keels on the upper part and with a few transverse veinlets, 3-nerved in each wing with transverse veinlets, glabrous except for the ciliate keels and truncate upper margin between them; lodicules 3, rhomboid above with a broad base, 1,8–2,4 mm long, thickened on the lower half and thin above with densely ciliate margins, the single posterior lodicule similar in all ways to the anterior pair except a little smaller; stamens 3, the anthers orange, 7,2–8,5 mm long, with the filament attached to the connective on the lower 1/4-1/5; ovary with 3 short stigmas (plumose ?); fruit not seen.

Specimens examined:

O.F.S.—Without precise locality: Drakensberg range, *Putterill s.n. sub Medley Wood 11336 (=Galpin 8576)* (PRE; US fragment ex NH). 2828 (Bethlehem): SE of Visierskerf, ± 15 km W of Fouriesburg (–CA), *Scheepers 1863* (PRE), Franshoek

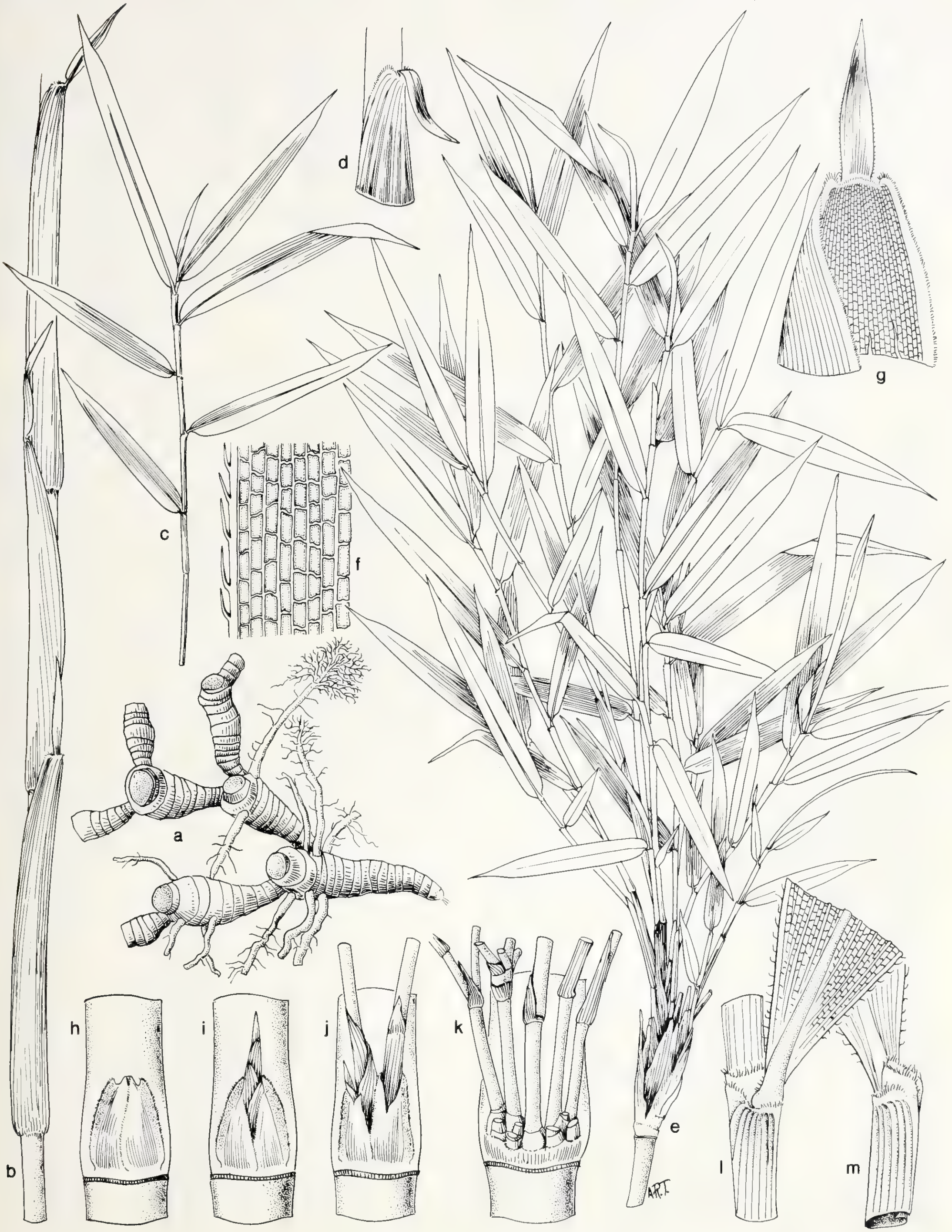

FIG. 1.—Vegetative features of *Thamnocalamus tessellatus*: a, rhizomes, somewhat diagrammatic (from photograph); b, new culm showing erect blades, × 0,5; c, leaf complement, × 0,5; d, summit of culm leaf showing reflexed blade, × 0,5; e, branches with foliage, × 0,5; f, section of leaf blade showing cartilaginous margin and tessellate venation, × 12,5; g, new culm leaf, inside view, × 1,5; h, branch bud covered by prophyllum, × 1; i, bud emerging through prophyllum as primary branching, × 1; j, young primary and secondary branches, × 1; k, branch complement, × 1; l, under part of foliage leaf showing outer and inner ligules, × 4,5; m, upper part of foliage leaf showing outer and inner ligules, × 4,5. (All figures from *Soderstrom & Du Toit* 2610 except c from *Van Zinderen Bakker* 13 and e, f, l and m from *Codd & Dyer* 2778. Illustration by Alice R. Tangerini).

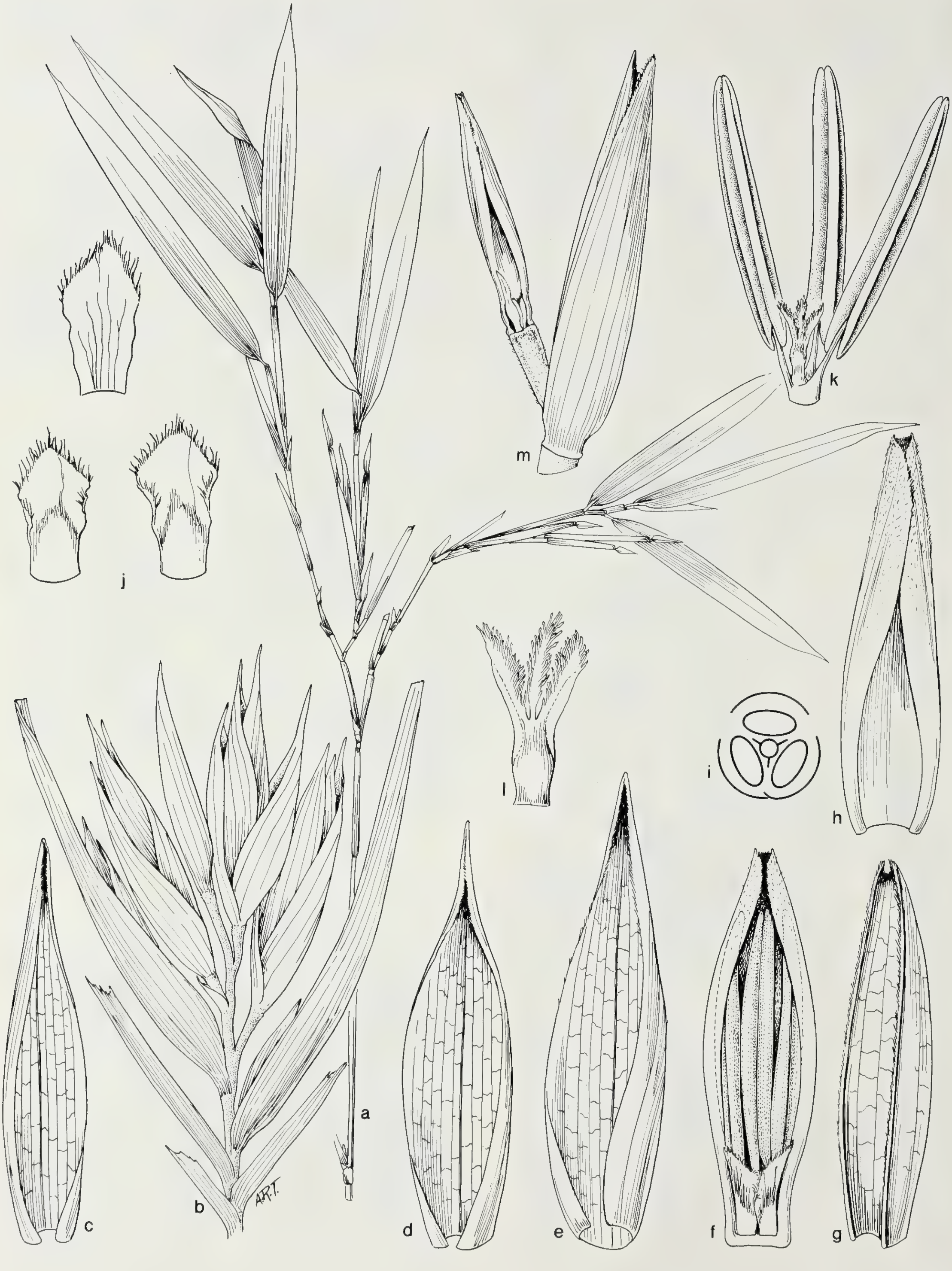

FIG. 2.—Flowering features of *Thamnocalamus tessellatus*: a, branch at commencement of flowering with small leaf blades that precede spikelet formation, × 0,5; b, spikelet, × 3; c, glume 1, × 6; d, glume 2, × 6; e, lemma, × 6; f, palea, front view, showing the anterior pair of lodicules with overlapping margins and enclosed anthers, × 6; g, palea, back view, showing the two strong keels, × 6; h, palea, front view, × 6; i, schematic of flower in cross section showing 3 lodicules, 3 stamens and ovary with 3 stigmas; j. lodicules, × 12,5; k, stamens and pistil, × 6;1, gynoecium, showing the 3 stigmas, × 15; m, upper part of spikelet with 2nd, 3rd and 4th florets, the 4th a rudimentary flap of tissue enclosed within the small lemma of the 3rd floret, × 6. (Fig. 2a based on *Killick* 1863, b–m on *Medley Wood* 11336 (= *Galpin* 8576). All drawings rendered by Alice R. Tangerini).

Farm, Ficksburg, *Loxton & Ellis 990* (PRE). 2829 (Harrismith): Platberg, Harrismith (−AC), *Putterill* (?) (PRE); Maweni Heights (−BD), *Van Zinderen Bakker 13* (PRE).

NATAL.—2828 (Bethlehem): Royal Natal National Park (−DB), *Codd & Dyer 2778* (PRE); Mont aux Sources (−DD), *Mogg 422* (PRE), *Hutchinson, Forbes & Verdoorn 54* (PRE). 2829 (Harrismith): Cathedral Peak Forestry Reserve (−CC), *Killick 1893* (PRE), *Soderstrom & Du Toit 2610* (PRE, US). 2929 (Underberg): Giants Castle Game Reserve (−AB), *Symons 150* (PRE), *Sim 20517* (PRE); Highmoor Forest Station (−BC), *Ellis 3161* (PRE); Bushman's Nek (−CC), *Killick & Vahrmeijer 3976,* (PRE); Underberg Dist. (−CD), *McClean 739* (PRE).

LESOTHO.—2828 (Bethlehem): Matalane River, Leribe Dist. (−CC), *Dieterlen 279, 279a* (PRE). 2928 (Marakabei): Pitseng, Leribe Dist. (−AA), *Dieterlen 1010* (PRE), Meniaming Stream, *Jacot Guillarmod 2207* (PRE). 3027 (Lady Grey): upper Quthing River gorge, Makoae (−BD), *Schmitz 8315.* 3028 (Matatiele): tributary of Likhaibaning River (−AC), *Archibald 2750* (PRE); mountain side above Buffalo River waterfall (−CA), *Galpin 6931* (PRE).

CAPE.—3027 (Lady Grey): Wittebergen (−CA), *Drège s.n.* (US fragment ex W); Haskally below Mt Newton, Barkley East (−DC), *Acocks 23872* (PRE). 3126 (Queenstown): Bamboesberg (−AC), *Archibald 2810* (PRE); Shepstone Berg near Andriesberg (−DA), *Galpin 2616* (PRE). 3226 (Fort Beaufort): Katberg, Stockenstrom Div. (−DA), *Drège s.n.* (PRE fragment ex K); top of Gaika's Kop, Hogsback (−DB) *Archibald 01* (PRE); Victoria (−DD), *Morton s.n.* (PRE). 3227 (Stutterheim): Gxulu Kop, Keiskammahoek (−CA), *Story 3515* (PRE).

Hubbard and Vaughan (1940) listed a specimen *(Vaughan A.139)* as occurring on Mauritius but we have not seen this specimen.

MORPHOLOGICAL DISCUSSION

The Bergbamboes grows in loose tufts with the culms separated by the short necks of the rhizomes, which may be 25−30 cm long. The habit of growth is sympodial with each new rhizome eventually turning up into a culm, the intervening short and solid internodes without roots or buds except where they are enlarged in the transition zone to culm. In *Soderstrom & Du Toit* 2610, which was collected next to a stream, the thick roots terminated in a mass of fine roots (Fig. 1a) and the main part of the root itself was found to have air canals (Fig. 5). The senior author has also observed thick roots with air canals on another bamboo, *'Arundinaria' densifolia* Munro, which occurs in marshes in the highlands of Sri Lanka.

The new culms are maroon and smooth, covered by culm leaves in which the blade is at first ascending (Fig. 1a), then becoming horizontal to reflexed (Fig. 1d). The culm leaf, a pale maroon when fresh, soon dries and becomes stramineous, eventually falling off. The culm leaf, especially the sheath and foliage leaf-blades are strongly marked by cross veins. This tessellate venation, which also occurs in the glumes, lemma, and palea, is the basis of the specific epithet. Branching occurs on the upper part of the culm with a cluster of stiff subequal branches at each of the nodes (Fig. 1e). The naked culms, each with a panache of foliage above, contributes to the highly ornamental appeal of this bamboo.

The mature branch complement (Fig. 1k) consists of several stiff subequal branches that emanate from the culm at about a 45 degree angle. The bases of the major 5 or 6 branches form a line just above the nodal line itself. A study of the developmental stages reveals that a single bud at the node (Fig. 1h) produces a primary axis (Fig. 1i) and soon thereafter two secondary axes (Fig. 1j). The primary axis pushes through the apex of the flaps of the prophyllum that have covered and protected the bud. The two secondary axes split the prophyllum during their growth and these ultimately remain as flaps of tissue on either side of the branch complement. The secondary branches arise in succession from the lower nodes of the primary axis and each bears a prophyllum. The prophyllum is the modified sheath of the first node of the axis and in our bamboo it subtends a bud capable of producing another branch. Tertiary axes develop from buds subtended by prophylla. Tertiary axes (Fig. 3b & d) develop at the nodes above the prophyllum and are subtended by a sheath.

The growth of all axes occurs rapidly and almost simultaneously and in the early stages the new branches are mixed with prophylla and subtending sheaths.

In the accompanying diagram (Fig. 4) the branching system is shown in 2 dimensions. Some subtending sheaths are either lacking or were not located in the dissection: we have indicated these by dotted lines. The lower nodes of the major axes run close together in reality and are not clearly marked as in this diagram. An occasional bract was found without a bud: either it was lacking or not well developed.

The pattern appears to be that the first (prophyllate) and the second nodes of the single primary axis and two secondary axes bear buds that develop into axes (those of the primary giving rise to the two secondaries and the secondaries giving rise to four tertiaries). In the diagram (Fig. 4) one branch of 4th order has begun to develop and another is beginning to develop at the prophyllate node of the third. If a 4th order branch develops at the prophyllate node of each tertiary branch the total number of developed axes in the branch will be 11. Theoretically a greater or lesser number can develop but this number seems to be average in this bamboo, probably because of space limitations.

The stiff foliage is quite resistant to wilting; even an hour and a half after severing the branches and exposure to full sun the leaves do not begin to curl. In most bamboos wilting occurs immediately or very shortly after cutting. The leaf blades have a scabrous cartilaginous margin and grill-like appearance due to the numerous and strong transverse veinlets (Fig. 1f).

The first signs of flowering come with the diminution of the leaf blades, as shown in Fig. 2a. The ultimate nodes of the branch bear spikelets, the lower ones of which may be subtended by a leaf sheath and the upper ones by a bract, or reduced leaf sheath. The uppermost spikelets are not subtended by a bract. The whole cluster of spikelets (Fig. 2b) is covered by long leaf sheaths from the lower nodes: these at first bear tiny blades that are deciduous, leaving the summit of the sheath truncate.

Ultimately all branches bear spikelets and few leaves, these falling away with the development of

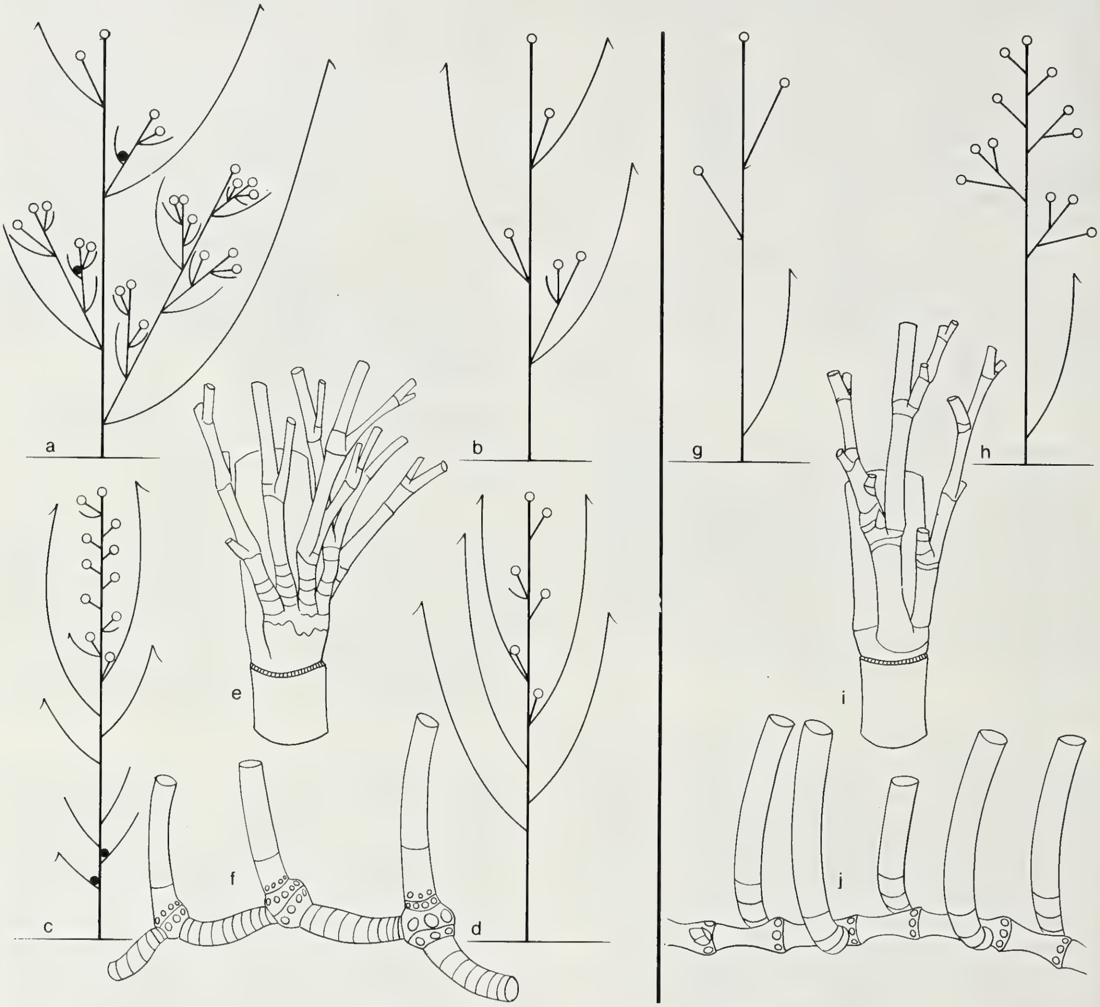

FIG. 3.—Schematic of the inflorescence, rhizome and branching patterns of *Thamnocalamus tessellatus* and related taxa compared with *Arundinaria gigantea*: a & b, inflorescence of *Thamnocalamus spathiflorus;* c, inflorescence of *Thamnocalamus spathaceus,* d, inflorescence of *Thamnocalamus tessellatus;* e, branch complement of *Thamnocalamus;* f, sympodial rhizome system of *Thamnocalamus* showing the short internodes of the neck and absence of buds or roots except in the transition zone; g, inflorescence of *Arundinaria gigantea;* h, inflorescence of *Sasa paniculata;* i, branch complement of *Arundinaria* (the *Sasa* type is not shown); j, monopodial rhizome system of *Arundinaria* showing that each node has a bud and roots. Open circles represent a spikelet and closed circles a bud, curved lines with hooks a sheath with blade and curved lines only a reduced sheath (bract).

the inflorescence and doubtless leading to death of the plant after flowering and seed-set. As in many bamboos flowering is rare in this species and probably occurs at long intervals. The only flowering specimens I have seen are those of Mrs Putterill collected in 1908 (appearing variously as *Medley Wood* 11336 or as *Galpin* 8576) and of Killick, collected in 1953.

The spikelets are 4-flowered, with the lower two florets best developed and reduction occurring in the 3rd and 4th (Fig. 2m). Stapf (1908) erred in referring to the spikelets as 2-flowered. The spikelet contains 2 glumes (Fig. 2c & d) and the floret a lemma (Fig. 2e) and palea (Fig. 2f–h). All of these organs are many-nerved and with numerous transverse veinlets.

The flower consists of 3 lodicules (Fig. 2j), of the type that is most common in bamboos — apex pointed, margins ciliate, and numerous vascular bundles. The posterior lodicule is similar to the anterior pair and little reduced as is so often the case in bamboos.

The androecium consists of three basifixed anthers (Fig. 2k) and gynoecium of an ovary with 3 stigmas (Fig. 2k & 1). These are small in the few spikelets available for dissection but are bristly and are apparently of the plumose type, which condition would become more apparent after elongation.

ANATOMICAL DESCRIPTION

The root in transverse section

Epidermis: uniseriate; epidermal cells thin walled

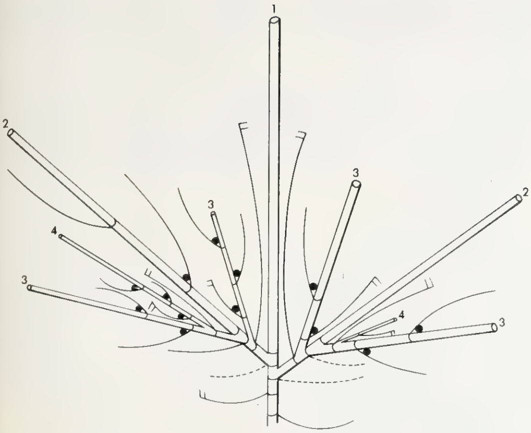

FIG. 4.—Schematic of branch complement in *Thamnocalamus tessellatus*.

and lacking cuticle. Root hairs absent. *Exodermis*: cells of outer subepidermal layers of cortex suberized and slightly thickened to form exodermis (Fig. 5a). Intergrades into cortex. *Cortex*: consists of inflated parenchyma cells of uniform size but becoming smaller externally and intergrading into exodermis (Fig. 5a & b); lack chloroplasts but few crystals present. Elongated radially orientated AIR CANALS located adjacent to the central cylinder; occupy about ⅔ the width of the cortex; conspicuous, numerous and regularly arranged (Figs. 5a & b). *Endodermis*: well-developed uniseriate cylinder of conspicuous cells with considerably thickened and lignified inner tangential and radial walls (Fig. 5b). No passage cells seen. *Vascular cylinder*: single layered sclerified pericycle surrounds primary vascular tissue; phloem strands located on periphery of vascular cylinder external to the circle of protoxylem and metaxylem vessel members; metaxylem vessels very wide, circular and thin walled. Centre of cylinder occupied by a pith containing a single large air canal (Fig. 5a).

The leaf blade in transverse section

Leaf outline: expanded; flattened to loosely inrolled from one margin only. *Ribs and furrows*: slight adaxial undulations with no regular pattern associated with the vascular bundles. Definite but slight abaxial ribs and furrows present; may be better developed than on adaxial surface; rib development opposite first order vascular bundles usually greater and composed of sclerenchyma girder. *Midrib*: SINGLE FIRST ORDER VASCULAR BUNDLE ONLY; projects abaxially; no adaxial development of amphivasal bundles (Fig. 6a). *Vascular bundle arrangement*: 7, 9, 11 or 13 first order vascular bundles in section (including median vascular bundle). 5 THIRD ORDER VASCULAR BUNDLES BETWEEN CONSECUTIVE FIRST ORDER VASCULAR BUNDLES; no second order vascular bundles; first order vascular bundles located in centre of blade; third order vascular bundles located closer to the abaxial surface (especially noticeable in freshly fixed material). *Vascular bundle description*: third order vascular bundles elliptical in shape; xylem and phloem distinguishable; first order vascular bundles rounded in outline; lysigenous cavity protoxylem vessel present; metaxylem vessels circular; diameter greater than width of parenchyma sheath cells. *Vascular bundle sheaths*: first order vascular bundle sheaths double (Fig. 6c); outer sheath horse-shoe-shaped with wide abaxial interruption; slight adaxial interruption. No extensions present; cells elliptical, often irregular in size; considerably smaller, but with thicker walls, than the mesophyll cells; chloroplasts absent or considerably fewer than in mesophyll cells. Inner sheath complete; cells with uniformly and heavily thickened walls. 3 SHEATH-LIKE LAYERS PRESENT IMMEDIATELY OUTSIDE THE METAXYLEM VESSELS in all specimens examined (Fig. 6b & c). *Sclerenchyma*: adaxial and abaxial girders associated with all vascular bundles; narrow towards bundle (particularly the adaxial girders) and especially well developed in association with the first order vascular bundles. All fibres with very thick walls; lumens almost excluded. No sclerenchyma between bundles. Small rounded sclerenchyma cap at margin. *Chlorenchyma*: comprised of ARM CELLS; INVAGINATIONS OF EQUAL LENGTH and from all directions in abaxially located cells but tend to be vertically arranged in uppermost adaxial layer (this distinction not very conspicuous) (Fig. 6c). FUSOID CELLS (cavities) present on either side of all vascular bundles; narrow, tapering gently, horizontal or downward projecting (Fig. 6b & c). Successive fusoid cells separated by 1 or 2 arm cells. *Colourless cells:* absent. *Adaxial epidermis*: bulliform cell groups fan-shaped with central cell equal in size to ½ leaf thickness; central cell inflated, fan-shaped. Located between all vascular bundles. Epidermal cell outer walls covered by a continuous, thick cuticle. NO PRICKLES, hooks, macro hairs or PAPILLAE. *Abaxial epidermis*: no bulliform cells occur; each epidermal cell covered by individually thickened cuticle projecting into thickened, narrow papillae; more than 1 papilla per cell (Fig. 6c). No macro-hairs. Large prickles common opposite the vascular bundles as well as between them (Fig. 6c).

Abaxial epidermis

Intercostal long cells: elongated; anticlinal horizontal walls parallel; end walls vertical; unthickened; moderately to deeply undulating with undulations U-shaped. Cell shape constant throughout intercostal zones. Hooks or micro-hairs present between successive long cells. No bulliform cells present. *Stomata*: low dome-shaped to parallel-sided; 6 rows of stomata in each intercostal zone restricted to 3 adjacent files adjoining the costal zones. SUNKEN IN PITS OVERARCHED BY PAPILLAE (Fig. 7a). *Intercostal short cells*: unsilicified with crenate outline; between virtually all long cells; bases for hooks and micro-hairs. *Papillae*: small, thickened cuticular papillae on all intercostal cells; many per cell; IRREGULARLY ARRANGED (not in rows); all similar in size and shape. OCCUR ON BASES OF HOOKS, intercostal short cells and overarch the stomata. Mainly intercostal but sometimes present on costal long cells of narrow costal zones overlying third order vascular bundles. *Prickles*: bases large (twice as long as stomata); short barbs all oriented in same direction (distal?). Costal, frequent especially on narrow costal zones; in same files as silica bodies. *Hooks:* circular bases about same diameter as stomata; short barbs pointing in all directions; common throughout intercostal zones (Fig. 7a). *Micro-hairs*: bicellular; BASAL CELL 3× LENGTH OF DISTAL CELL (Fig. 7a); both cells markedly elongated; about 4x length of stomatal complexes; base not constricted at point of attachment; emerge straight out of short cell; restricted to centre of intercostal zones. *Macro-hairs*: none seen. *Silica bodies*: TALL,

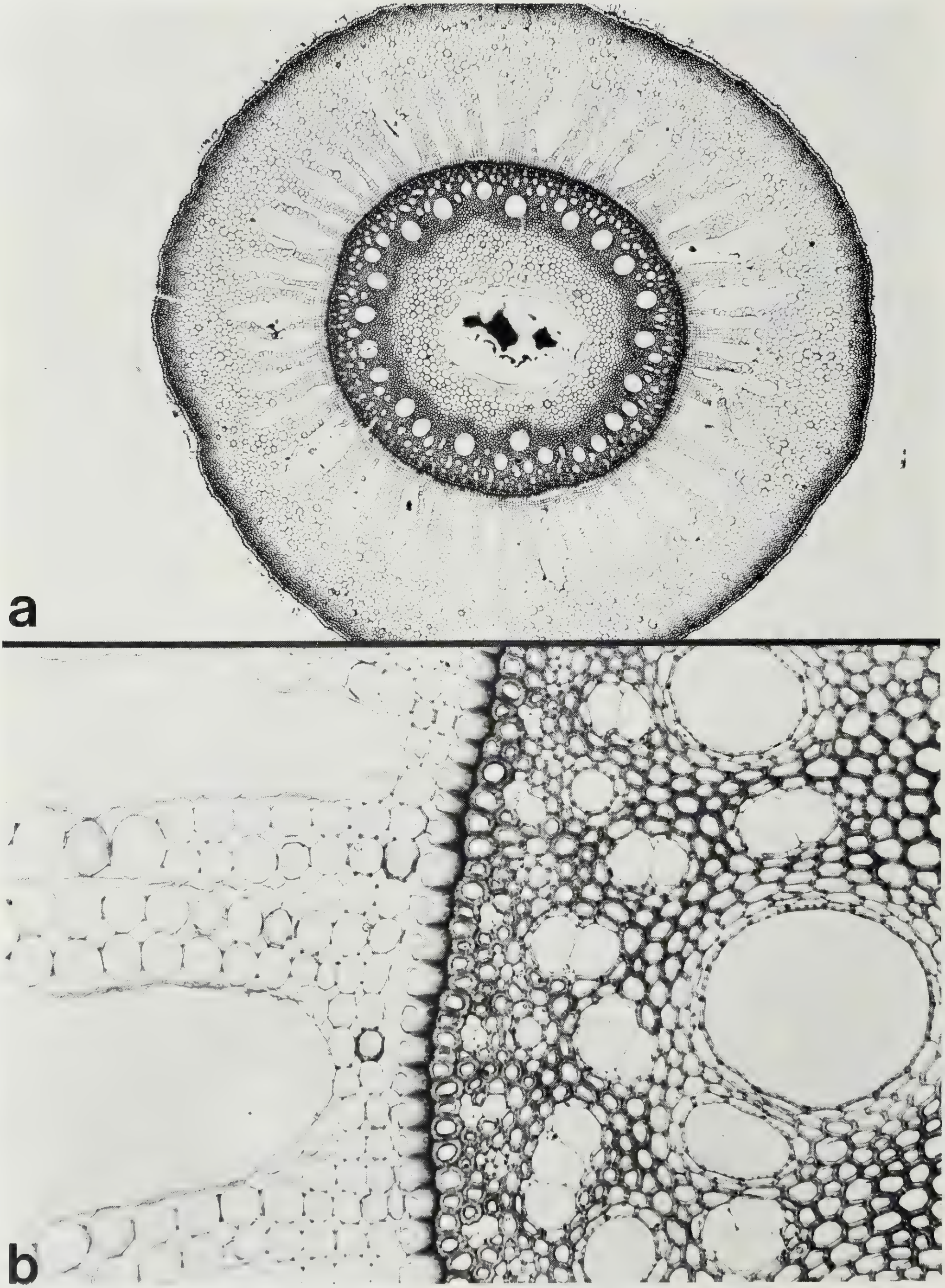

FIG. 5.—Transverse sections of the root of *Thamnocalamus tessellatus*: *Soderstrom & Du Toit* 2610; a, × 40; b, × 400.

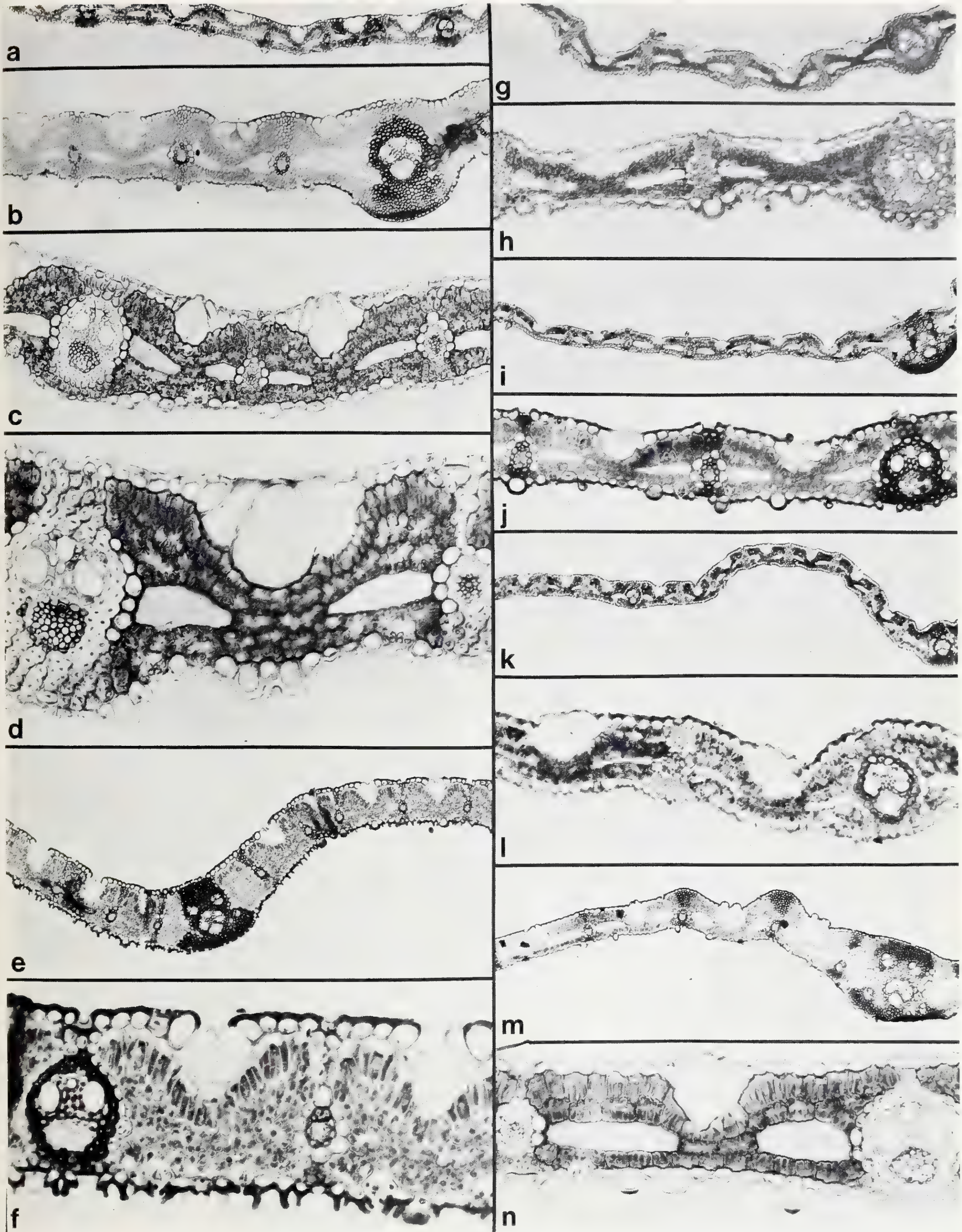

FIG. 6.—A comparison between the leaf blade anatomy of *Thamnocalamus tessellatus* and various other bamboos: a–d, *T. tessellatus*; a, *Soderstrom & Du Toit* 2610, × 100, note five small vascular bundles between consecutive first order bundles; b, *Ellis* 3161, × 160, simple midrib containing single vascular bundle; c, *Soderstrom & Du Toit* 2610, × 400; d, *Soderstrom & Du Toit* 2610, × 640, invaginations of arm cells not vertically orientated. Papillae absent on adaxial surface; e–f, *Phyllostachys aurea, Ellis* 3511; e, × 100, midrib with first order bundle and two small vascular strands; f, × 400, fusoid cells absent and note vertical orientation of adaxial mesophyll cells and well developed abaxial cuticular papillae and prickles; g–h, *Thamnocalamus spathiflorus, McClure* 22006; g, × 160, midrib with single vascular bundle; h, × 400, mesophyll poorly preserved but note minute adaxial papillae; i–j, *Arundinaria gigantea*; i, *Soderstrom* 2530, × 100, midrib with complex vasculature and 7 bundles between larger bundles; j, *Soderstrom & Calderon* 2047, × 400, leaf much narrower than that of *T. tessellatus* (Fig. 6c); k–l, *Arundinaria alpina, Greenway & Kanuri* 13638; k, × 100, midrib of single vascular bundle only but 7 smaller bundles between consecutive larger bundles; l, × 400; m–n, *Bambusa balcooa, Smook & Soderstrom* 1982; m, × 160, complex midrib vasculature; n, × 400, arm cell invaginations vertically orientated.

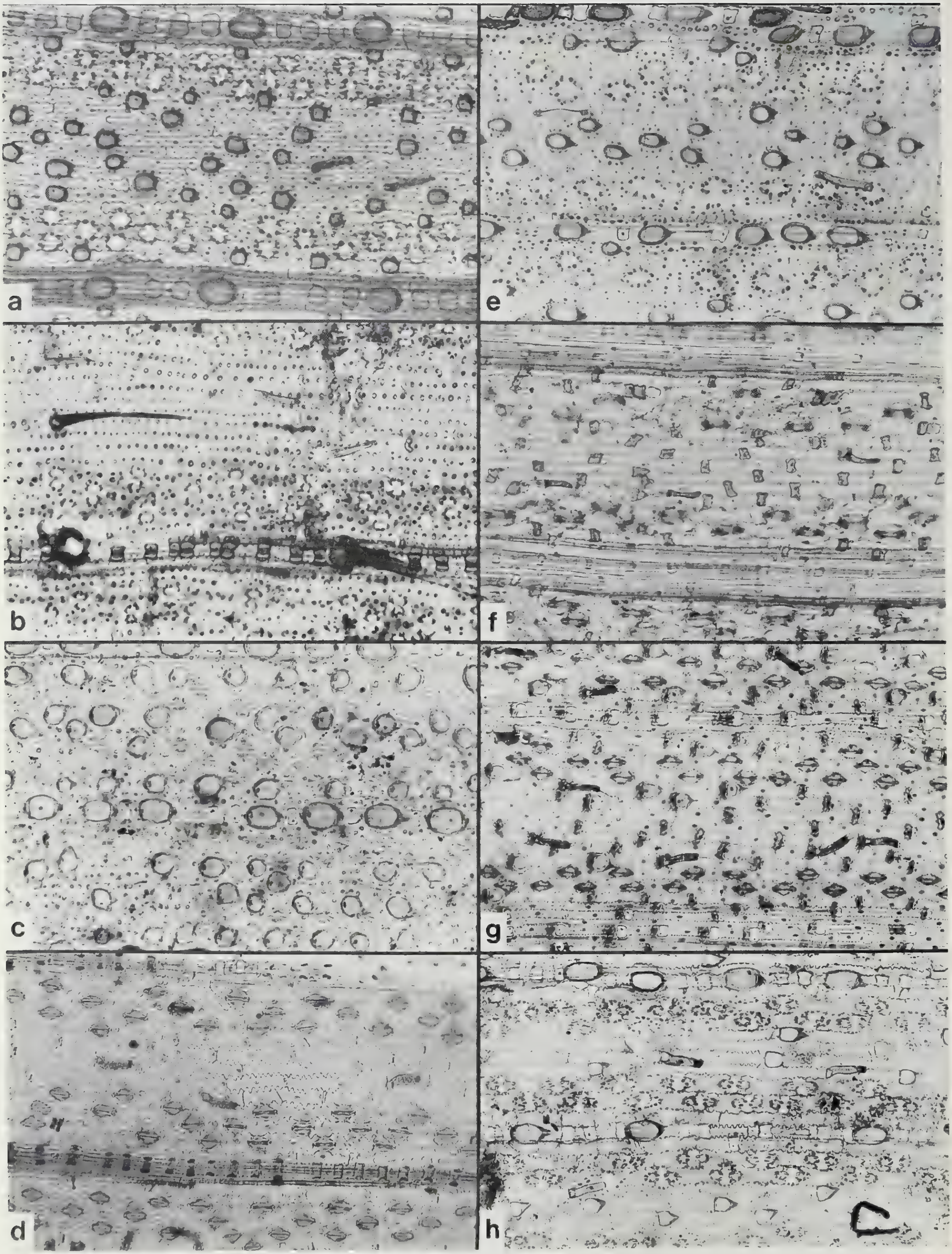

FIG. 7.—Abaxial epidermal structure of *Thamnocalamus tessellatus* compared with various other bamboos. All × 400: a, *Thamnocalamus tessellatus, Soderstrom & Du Toit* 2610, note saddle shaped silica bodies, prickles and hooks, papillate intercostal long cells with papillae overarching stomata and elongated basal cells of microhairs; b, *Arundinaria gigantea, Soderstrom* 2530, costal and intercostal macro-hairs present; c, *Phyllostachys aurea, Ellis* 3511, hooks abundant and micro-hairs very small; d, *Oxytenanthera abyssinica, Smook & Soderstrom* 1983, hooks and prickles absent and intercostal long cells with undulating cell walls; e, *Thamnocalamus spathiflorus, McClure* 22006, very similar to *T. tessellatus* except that some silica bodies are dumb-bell shaped; f, *Arundinaria alpina, Greenway & Kanuri* 13638, papillae absent on this part of the leaf blade; g, *Bambusa balcooa, Smook & Soderstrom* 1982, undulate intercostal long cell walls; h, *Chimonobambusa marmorea, Makino s.n.*, cells of micro-hair of equal length.

SADDLE-SHAPED to square with angular outlines. Granules present. Same width as adjacent long cells. *Costal cells*: files of costal long cells alternate with files of alternating silica cells and costal short cells (and prickles). About 7 files comprise first order vascular bundle costal zones and 3–5 files third order vascular bundle costal zones.

Compiled from the following material:

Loxton & Ellis 990: 2828 (Bethlehem): Ficksburg (–CA). *Soderstrom & Du Toit 2610:* 2829 (Harrismith): Cathedral Peak (–CC). *Ellis 3161:* 2929 (Underberg): Highmoor (–BC). *De Wet 1124:* collection locality unknown but doubtless S. Africa.

ANATOMICAL DISCUSSION

To enable an assessment of the relationships of *T. tessellatus* to be made, the leaf anatomy of the Bergbamboes has been compared with various other bamboo species. The results of this comparative study are presented graphically in Table 1. Anatomical characteristics of the leaf in transverse section and of the abaxial epidermis, which in combination appear to be diagnostic of *T. tessellatus,* have been used for this comparison and have been printed in block capitals in the preceding anatomical description.

It is immediately evident from Table 1 that no single character distinguishes *T. tessellatus* from all the other bamboo species in the sample studied. In fact there appear to be no diagnostic characters separating any of the genera or species examined and combinations of different characters are the only effective means of distinguishing any of the taxa examined. Even the presence of fusoid cells, which is generally considered to be characteristic of the bambusoid grasses (Brandis, 1907; Chih-Ying Wu, 1958; Metcalfe, 1960; Calderon & Soderstrom, 1973) is not consistent throughout the sample studied and *Phyllostachys aurea* A. & C. Riv. (Fig. 6f), *Chimonobambusa marmorea* (Mitf.) Makino and *C. falcata* (Nees) Nakai lack fusoid cells completely. Arm cells are present in all taxa studied but these structures are not exclusive to these woody bambusoid grasses but also occur in the herbaceous bambusoid (Calderon & Soderstrom, 1973), oryzoid

SPECIES	VOUCHER SPECIMEN COLLECTORS NUMBERS	MIDRIB		NO OF 3°VBS BETWEEN CONSECUTIVE 1°VBS		FUSOID CELLS			ARM CELL INVAGINATIONS		ADAXIAL EPIDERMAL PAPILLAE		ADAXIAL APIDERMAL PRICKLES		ABAXIAL STOMATA		ABAXIAL PAPILLAE		ABAXIAL PAPILLAE ARRANGEMENT		MICRO-HAIR BASAL CELL LENGTH		SILICA BODIES		
		COMPLEX OF VBS	SINGLE VB ONLY	MORE THAN 5	5 3° VBS	ABSENT	NOT NEAR MARGIN	PRESENT	VERTICAL FROM LOWER WALL	RADIAL FROM ALL WALLS	PRESENT	ABSENT	PRESENT	ABSENT	NOT OVERARCHED BY PAPILLAE	OVERARCHED BY PAPILLAE	HOOKS WITHOUT PAPILLAE	ON BASES OF HOOKS	SINGLE ROW	IRREGULAR	LESS THAN 3X DISTAL CELL	3X LENGTH OF DISTAL CELL	DUMB-BELL SHAPED	SADDLE SHAPED TALL	SADDLE SHAPED
Thamnocalamus tessellatus	Loxton & Ellis 990		■		■			■		■		■		■		■		■		■		■			■
	Ellis 3161		■		■			■		■		■		■		■		■		■		■			■
	Soderstrom & Du Toit 2610		■		■			■		■		■		■		■		■		■		■			■
	De Wet 1124		■		■			■		■		■		■		■		■		■		■			■
Thamnocalamus spathiflorus	McClure 22006		■		■			■		■	■			■		■		■		■		■	■		■
Thamnocalamus aristatus	Emery 133	■		■				■	■		■			■		■		■		■	■		■		
Arundinaria alpina	Greenway & Kanuri 13638		■	■				■		■		■		■		■		■		■	■				■
Arundinaria amabilis	Soderstrom 2526	■		■				■	■			■		■		■		■		■					■
Arundinaria auricoma	Kew slide 1953	■		■				■	■			■	■			■		■		■					
Arundinaria gigantea	Soderstrom 2530	■		■				■		■		■	■			■		■	■			■			■
	Soderstrom & Calderon 2047	■		■				■		■		■	■			■		■	■			■		■	
Arundinaria japonica	Kew slide 1953	■		■				■		■		■		■		■		■		■					
Arundinaria maling	Emery 146	■		■			■		■		■		■			■		■	■		■			■	
Arundinaria sp	Soderstrom 2500	■		■	■			■	■			■		■		■		■		■	■			■	
Sinarundinaria nitida	McClure 21148		■	■			■			■		■	■			■		■		■		■	■		
Chimonobambusa falcata	Soderstrom 2255	■		■		■				■	■			■	■		■			■	■			■	
Chimonobambusa khasiana	Soderstrom 2599	■		■				■	■			■		■		■		■	■			■		■	
Chimonobambusa marmorea	Makino s.n.	■		■		■				■		■		■		■		■		■	■				■
Oxytenanthera abyssinica	Smook & Soderstrom 1983	■		■				■	■			■	■			■		■		■	■			■	
Bambusa balcooa	Smook & Soderstrom 1982	■		■				■	■			■		■		■		■	■		■			■	
Phyllostachys aurea	R. Ellis 3511	■		■		■				■		■		■		■		■		■		■		■	

TABLE 1.—Comparison of the leaf anatomy and epidermal structure of *Thamnocalamus tessellatus* and the other bamboo species examined in this study

(Tateoka, 1963) and some arundinoid grasses (Gordon Gray & Ward, 1971; Clifford & Watson, 1977).

The possession of a conspicuous midrib, containing a complex vascular system, is another anatomical feature which is considered to be characteristic of the bambusoid type of leaf anatomy (Metcalfe, 1960; Calderon & Soderstrom, 1973). Exceptions to this condition have been observed in this study and Table 1 shows that the Bergbamboes has a simple midrib (Fig. 6b) as has *Thamnocalamus spathiflorus* (Trin.) Munro (Fig. 6g), *Arundinaria alpina* K. Schum. (Fig. 6k) and *Sinarundinaria nitida* (Mitf.) Nakai. *T. tessellatus,* therefore, shares this significant characteristic with *T. spathiflorus,* a fact which supports their placement in the same genus. *Thamnocalamus* is not homogenous for this character, however, as *T. aristatus* (Gamble) E. G. Camus has a complex vasculature of the midrib. The simple midrib condition is consequently not diagnostic of the genus and, in addition, also occurs in *Arundinaria* and *Sinarundinaria.*

The character which comes closest to being diagnostic of *T. tessellatus* is the number of third order vascular bundles between successive lateral first order bundles. There are 5 of these smaller bundles between consecutive larger bundles in *T. tessellatus* (Fig. 6a) and *T. spathiflorus* whereas the other species studied have 7 or more. An exception is an undescribed *Arundinaria* sp. (Table 1) which also only has 5 smaller bundles. Once again this characteristic is not exclusive to *Thamnocalamus* and within the genus, *T. aristatus* differs from the other two species studied with respect to this character. Furthermore, this attribute is not completely reliable and is dependent on the position along the width of the leaf blade at which it is determined and tends to be somewhat variable, particularly towards the margin.

Anatomically the Bergbamboes resembles *T. spathiflorus* most closely (Table 1), the only difference being the presence of minute papillae (Fig. 6h) and dumb-bell shaped silica bodies (Fig. 7e) on *T. spathiflorus.* Neither of these differences is absolutely consistent, however, and, consequently little taxonomic emphasis has been placed on them. Thus *T. spathiflorus* also has saddle-shaped silica bodies (Fig. 7e) in addition to the dumb-bell shaped bodies and in this respect resembles *T. tessellatus.* The possession of papillae appears to be inconsistent and sometimes only one half of the lamina is papillate (either adaxially or abaxially) and the other not or papillae may be absent laterally but present in the region of the midrib. This variable condition is clearly illustrated by the example of *Arundinaria alpina* where the abaxial epidermal preparation is clearly without papillae (Fig. 7f) whereas, they are present on the abaxial epidermal cells of the transverse section (Fig. 6l) prepared from a different leaf from the same plant. This character is, therefore dependent on the part of the leaf blade studied and differences in the number and distribution of these intercostal papillae are consequently of limited taxonomic significance and not of specific diagnostic value as has been reported (Ghorai & Sharma, 1980). For these reasons it is concluded that the Bergbamboes shows closer anatomical relationships with *T. spathiflorus* than with any of the other bamboos studied and these slight differences are considered to be of little consequence.

The lack of anatomical conformity in the genus *Thamnocalamus,* after the inclusion of the Bergbamboes, appears most unsatisfactory and possibly implies that taxonomic adjustment may be required. *T. tessellatus* and *T. spathiflorus* show close anatomical agreement but *T. aristatus* differs significantly. However, it must be realized that generic characters of the woody bamboos are not well defined and species within the same genus can show greater differences than with species belonging to different genera. The decision to transfer the Bergbamboes to *Thamnocalamus* was based on our combined comparative anatomical and morphological studies and although the inference may be drawn from Table 1 that anatomically *T. tessellatus* closely resembles *Arundinaria alpina* these species differ substantially in gross morphology, spikelet and inflorescence structure. The anatomy of the Bergbamboes and *A. gigantea* (Walt.) Muhl., the type species of the genus, shows many significant differences such as the midrib structure (Fig. 6i), leaf thickness (Fig. 6j) and epidermal macro-hairs (Fig. 7b). On these grounds the removal of the Bergbamboes from *Arundinaria* is obviously justified but the placement of *A. alpina* warrants review in light of the anatomical similarities with *T. tessellatus* and the fact that they are both African species.

An observation, which has not been incorporated in Table 1, but which is of considerable interest and contrary to published information is the presence of three sheath layers surrounding the first order bundles of *T. tessellatus.* Double bundle sheaths have been reported for the Bambuseae (Brown, 1958; Metcalfe, 1960; Calderón & Soderstrom, 1973) but Fig. 6d clearly illustrates that three sheath-like layers are present externally to the metaxylum vessels — two mestome-like layers and the parenchyma sheath. These three sheath-like layers were also observed in *T. spathiflorus* (Fig. 6h), *Arundinaria gigantea* (Fig. 6j) and *Bambusa balcooa* Roxb. (Fig. 6n) and appear to be a common feature of these woody bamboos.

CONCLUSIONS

Our quest to establish the relationships of the Bergbamboes has led to a comparative study of its leaf anatomy, gross morphology, spikelet and inflorescence. The results indicate that this bamboo was originally misplaced in *Nastus* and subsequently so in *Arundinaria.*

The leaf anatomy of the Bergbamboes is bambusoid and specifically of the type found in the woody bamboos (Calderón & Soderstrom, 1973). Our studies have been made on many widely divergent genera and the results have corroborated the statement of Metcalfe (1960: 540), that '. . . the bamboos form a remarkably homogeneous group so far as the structure of their leaves is concerned'. It is immediately evident that there are no mutually exclusive characters separating any of the genera studied and generic anatomical characters appear to be difficult to find or not to exist. Even the presence or absence of what would appear to be a significant character, such as fusoid cells, seems to be meaningful only at the specific level, as in *Chimonobambusa,* for example. We were unable to find any character that is diagnostic of any species to the exclusion of all others. The dumb-bell-shaped silicabodies of *Thamnocalamus* seem to come closest; however, these bodies are rather irregular in shape and not distinct. In fact, *Thamnocalamus spathiflorus* seems to match our Bergbamboes more closely than any other species examined, differing only in the presence of adaxial papillae. The adaxial epidermises of these two species therefore look considerably different but show similarities in all other respects, including silica body shape.

A great deal of attention has been given to the use of vegetative characters in bamboo classification due to the rarity of flowering in this group of grasses and lack of spikelets and inflorescences for study. Significant at the generic level are the type of rhizome system and branching pattern. For example, the Bergbamboes and *Nastus* have sympodial rhizomes while *Arundinaria* possesses a monopodial one. The branching of all three is distinct: *Nastus,* as exemplified in the type, *N. borbonicus,* produces a large cluster of subequal branches at the nodal line (perhaps derived from more than one bud as in the putatively related *Chusquea?*); *Arundinaria,* as exemplified in the type, *A. gigantea,* produces a single branch at the node with each node in turn giving rise to a single branch; while the Bergbamboes produces a primary branch that gives rise almost immediately to secondary and tertiary axes that result in a row of sub-equal branches above the nodal line. The combination of rhizome and branching types, different in all three, implies that we are dealing with distinct genera.

Our third avenue of inquiry, the spikelet and inflorescence, confirms this implication. The spikelet of *Nastus* consists of a series of glumes, as many as five, that precede two fertile florets, these each containing a flower with three lodicules, six stamens, and three stigmas. On the contrary, the spikelets of the Bergbamboes and *Arundinaria* contain two glumes, which is common in most grasses, and several florets, the lowermost developed and uppermost reduced. The flower itself contains, in each case, a similar complement—three lodicules, three stamens, and an ovary with three stigmas.

The combination of sympodial rhizome, branching type, and spikelet type that is found in the Bergbamboes also occurs in the Sino-Himalayan genera, *Sinarundinaria* and *Thamnocalamus.* The inflorescence pattern, however, is quite different in these two, with that of the former an open panicle and that of the latter a bracteate racemiform structure as found in the Bergbamboes.

As shown diagrammatically in Fig. 3, the infloresence of the Bergbamboes (Fig. 3d) consists of several short-pedicellate spikelets covered by the elongated sheaths of subtending leaves. The lower leaves of the series contain no buds in their axils, while the upper ones (lower two of the inflorescence) contain a spikelet, somewhat aborted. The uppermost spikelets are without a bract or may bear a rudimentary one.

The same basic inflorescence pattern is found in the genus *Thamnocalamus.* As shown in the diagram of an inflorescence of the type species, *T. spathiflorus* (Fig. 3a), each spikelet is subtended by a bract. In the case of Fig. 3a, the terminal part of an inflorescence is shown and here the buds have developed into branches that have rebranched, each primary branch subtended by a leaf with a well-developed sheath and each secondary branch by a bract. In another part of the same inflorescence (Fig. 3b), the leaves with expanded sheaths subtend a single spikelet or branch. The degree of branching and development of buds varies at different nodes.

In *T. spathaceus* (Franchet) Soderstrom (Fig. 3c), the several leaves with well-developed sheaths develop close together, the lower ones subtending a bud, the upper ones empty. In the flowering stage, each branch terminates in an inflorescence, which consists of several leaves with expanded sheaths increasingly longer upwards, covering the inflorescence. The lowermost spikelet is subtended by a leaf with expanded sheath and the following spikelets (in the case shown, two) by bracts. Several succeeding spikelets are ebracteate except the penultimate.

All of these taxa are similar in having at least some bracteate spikelets and the tendency for them to be covered by leaves with well-developed sheaths. The most complex inflorescence shown is that of *T. spathiflorus*: variations in the extent of development of the buds could theoretically lead to the type we are observing in *T. spathaceus* and the Bergbamboes. All of these taxa possess a similar branching habit as depicted in Fig. 3e and sympodial rhizome system as depicted in Fig. 3f.

In contrast to these taxa is *Arundinaria gigantea,* type of the genus, whose monopodial rhizome system is depicted in Fig. 3j and branching pattern in Fig. 3i. The inflorescence is a raceme that is long-exserted and not covered by overtopping sheaths. Generally the lowermost spikelet is bracteate and the upper one(s) usually ebracteate or with tiny bracts as depicted in Fig. 3g. A related genus is *Sasa* in which the spikelets are arranged in a long-exserted panicle, shown in Fig. 3h. It also has monopodial rhizomes but a pattern of branching different from *Arundinaria* and not shown here. The inflorescence of *Sinarundinaria* is of the type represented by Fig. 3h, which is seen to be totally distinct from that of *Thamnocalamus.*

Based on present knowledge, we are assigning the Bergbamboes to the Sino-Himalayan genus, *Thamnocalamus,* in which the following five species are currently recognized: *T. spathiflorus* (Trin.) Munro, common in fir forests of north-west Himalayas above 7 000 ft; *T. aristatus* (Gamble) E. G. Camus, north-eastern Himalayas in eastern Nepal, Assam, Sikkim, and Bhutan, above 8 000 ft in temperate broadleaf forests; *T. spathaceus* (Franchet) Soderstrom, above 7 500 ft in fir forests of southern

Gansu, eastern Sichuan and western Hupeh provinces of China; *T. sparsiflorus* (Rendle) Keng f., above 8 000 ft in conifer woods in Hupeh Province of China; and *T. cuspidatus* (Keng) Keng f., from Kwangsi Province of China in woods at about 5 000 ft elevation.

The isolated occurrence of the South African member of *Thamnocalamus* is intriguing and raises the interesting question of how this came about. The nature of the bamboo plant, especially the infrequent flowering and production of seeds not adapted for long-distance dispersal, favours the assumption that the present-day distribution of these species reflects past land connections and overland migration. A few possibilities come to mind: 1) the genus evolved in west Gondwanaland and was present in Africa and on the Indian subcontinent prior to the latter's movement northward and abutment with the Asiatic landmass, speciation occurring in the newly forming Himalayas, leaving the South African element as a relict; 2) species of the genus migrated from the eastern Himalayas during the Miocene followed by deterioration in the climate and isolation in favourable mesophytic sites of the coastal and mountain belt that extends from the Cape to Natal; 3) migration occurred from the south in the Miocene reaching the Himalayas with subsequent extinction of taxa between there and South Africa.

Although there are no known bamboos of the *Thamnocalamus* alliance that occur between South Africa and the Himalayas, bamboos of the *Sinarundinaria* alliance do occur in Madagascar and in east Africa (under the name *Arundinaria)* and from the western Himalayas to the Phillippines (under the names *Arundinaria, Sinarundinaria,* and *Yushania),* indicating that such a distribution is not out of the question.

The isolated position in the United States of the canebrake, whose sibling species occur in eastern Asia, is reminiscent of the far-flung dominions of the Bergbamboes and its sibling species. While the South African-Himalayan disjunction may not be so clear, that of eastern United States and eastern Asia is well understood and documented. During warmer periods of the Tertiary, a continuous forest extended across the Northern Hemisphere from Asia to eastern North America. Ensuing cooler climatic conditions with the advance and retreat of glaciers, eliminated much of the forest, except in parts of Asia and eastern North America. Many genera today are common to both regions and reflect an Arcto-Tertiary distribution: *Celtis, Liriodendron, Magnolia,* and *Ulmus* are a few. Species of *Arundinaria* were doubtless understory plants in this forest, represented today by a single species in North America and many in eastern Asia. Such phytogeographical evidence for *Arundinaria* corroborates the viewpoint that the relationships of South Africa's endemic Bergbamboes are not to be found with this genus but elsewhere.

ACKNOWLEDGEMENTS

We are grateful to Dr Bernard de Winter, who facilitated the work of the senior author during his short visit to South Africa in February 1980, making it possible to visit a number of bamboo sites in the country. Collections of the Bergbamboes were made in collaboration with Mr Pierre du Toit (formerly Natal Herbarium), whose assistance is greatly appreciated, as well as that of Mr Coetzer, forest officer at the Cathedral Peak Forest Research Station in Winterton, Natal. Figures 1–4 were prepared by Alice Tangerini, to whom we are indeed grateful for such fine renderings.

UITTREKSEL

Thamnocalamus **tessellatus** *(Nees) Soderstrom & Ellis,* comb. nov. [= Arundinaria tessellata *(Nees) Munro*] *is die enigste inheemse Suid-Afrikaanse bamboessoort en kom in die oostelike distrikte van die Kaapprovinsie, deur Lesotho en Natal, tot in die oostelike Oranje-Vrystaat op hoogtes van omtrent 1 500–2 000 m voor. Die Bergbamboes is eers deur Nees in 1841 beskryf as 'n verteenwoordiger van die genus* Nastus *weens die ooreenkoms van die blompakkies met dié van* N. borbonicus. *Die Bergbamboes is later oorgeplaas na die omvattende genus van daardie tyd,* Arundinaria, *waarvan die tipe spesie endemies in die suidoostelike dele van die Verenigde State van Amerika is. Ons huidige kennis van die bamboesgenera dui aan dat die Suid-Afrikaanse spesie van* Nastus *uitgesonder kan word omdat die bloeiwyse nie 'n pluim is nie maar 'n tros met skudblare is, die vegetatiewe stingels word nie kransgewys gedra nie maar is 'n reeks halfgelyke stingels wat in 'n ry bokant die knoop gedra word en* T. tessellatus *het 'n meeldraadkrans van drie meeldrade en nie ses soos in* Nastus *nie. Die bergbamboes, wat simpodiale wortelstokke en verskeie halfgelyke stingels het, kan ook nie in* Arundinaria *gehou word nie, omdat monopodiale wortelstokke en 'n enkele stingel by die knoop kenmerkend van hierdie genus is. Die eenvoudige, uitgestote bloeiwyse, sonder skutblare, van* Arundinaria *is ook heeltemal kenmerkend van dié van die Bergbamboes.*

Om die Suid-Afrikaanse bamboes meer spesifiek te plaas het ons vergelykende studies van die blaaranatomie, epidermis en morfologie onderneem en die bloeiwyse en blompakkies ontleed. Die resultate van hierdie studie toon 'n opvallende ooreenkoms met verteenwoordigers van die Sino-Himalaja genus, Thamnocalamus. *Gevolglik is die Bergbamboes oorgeplaas na hierdie genus. Die resultate word saam met 'n interpretasie van die filogenetiese status van die Bergbamboes voorgelê en moontlike gebeurtenisse wat tot die skeiding van die spesies in die genus gelei het, word bespreek.*

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Notes on African plants

VARIOUS AUTHORS

APOCYNACEAE

CATHARANTHUS AND *VINCA* IN SOUTHERN AFRICA

A good deal of confusion regarding the correct name of *Catharanthus roseus* (L.) G. Don has existed in the past. This pantropical weed has been commonly, but incorrectly, referred to as *Vinca rosea* L. But, as Lawrence (1959), Farnsworth (1961) and Stearn (1973, 1975) have convincingly established that *Vinca* and *Catharanthus* are distinct genera, differing in 34 morphological characters, cytology, chemistry and geographical distribution, there should be no further confusion. *Vinca,* with six species, is native to Europe, western and central Asia and has become naturalized in North America, whereas *Catharanthus,* with eight species, occurs in Madagascar, with one of the species in India. One of its members *C. roseus* has become a pantropical weed. The genus *Vinca* was established by Linnaeus in 1753 when he described two species *V. minor* and *V. major.* In 1759 he added *V. rosea* (now the accepted lectotype of *Catharanthus).* This species was separated by Reichenbach (1828) as the genus *Lochnera.* This name remained a *nomen nudum* until Endlicher provided a description in his Genera Plantarum 583 no. 3406 (1838). The name is illegitimate, however, as it is a later homonym of *Lochneria* Scop. (1777) and a synonym of *Catharanthus* G. Don (1837). The correct citation for the Madagascan periwinkle is therefore as follows:

Catharanthus roseus *(L.) G. Don,* Gen. Syst. 4: 95 (1837)

Vinca rosea L., Syst. Nat. ed. 10,2: 944 (1759)

Lochnera rosea (L.) Spach., Hist. Nat. Veg. Phan. 8: 526 (1839)

Vinca gulielmi waldemarii Klotzsch in Klotzsch & Garcke, Bot. Reise Prinzen Ergebn. Waldem. 89, t. 70 (1862)

Ammocallis roseus (L.) Small, Fl. S.E.U.S. 935 (1903)

Vinca minor and *V. major* have also become naturalized weeds in South Africa. They can be separated from *Catharanthus roseus* as follows:

Corolla funnel-shaped (infundibular) with a gradually expanded tube, anthers with apical appendages; seeds 6–8, 6–10 mm long, brown; foliage persistent, evergreen:
  Calyx 3–5 mm long, glabrous .... *Vinca minor*
  Calyx 7–18 mm long, ciliate .... *Vinca major*
Corolla salver-shaped (salverform) with an almost cylindric tube, anthers without apical appendages; seeds 15–30, 1–3 mm long, black; foliage deciduous, not persisting .... *Catharanthus roseus*

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C. H. STIRTON

FABACEAE

A NEW SPECIES OF *INDIGOFERA* FROM THE SOUTH-WEST CAPE

Indigofera superba *C. H. Stirton,* sp. nov. subsectione *Psiloceratiae* Gillettii proxima.

Frutex erectus molliter lignosus ad 2 m altus; ramis in partibus superioribus ramificantibus, canoalbis, junioribus appressis strigulosis glabrescentibus. *Stipulae* liberae, subulato-setaceae. *Folia* regularia, imparipinnata. *Foliola* 9–11, 16–18 mm longa, 11–13 mm lata, suborbiculata ad late obovata, utrinque minute strigillosa semiconduplicata. *Inflorescentiae* axillares, racemosae densae, floribus multis, roseae. *Flores* 8–9 mm longi rosei, unoquoque bractea caduca filiformi 5–7 mm longa subtenti. *Tubus calycis* 2 mm longus, lobis 3plo breviore; lobis calycis omnibus linearibus, complanatis, villosis. *Vexillum* 8–8,5 mm longum, 4,2–4,7 mm latum, anguste ovatum. *Petala alarum* 8 mm longa, 2 mm lata. *Laminae* carinae 8 mm longae, 2 mm latae, manifeste saccatae. *Pistillum* 4,5 mm longum, glabrum sessile, ovulis 5–7. *Antherae* valde apiculatae, dorsifixae, squamis basalibus ad 0,5 mm longis; vagina stamineali 6 mm longa. *Fructus* cylindraceus (10)15–25 mm longus, 3 mm latus dehiscens; septa 2 mm lata, doliiformi, semina secedenti. *Semina* 2,25 mm lata et longaque, flavovirentia maculis purpurascentibus graduum variorum.

TYPE. — Cape, 3419 (Caledon): near Vogelpool, Vogelgat (–AD), *I. Williams 2439* (PRE, holo.!; K, iso!; NBG, iso!; Vogelgat Herbarium, iso!).

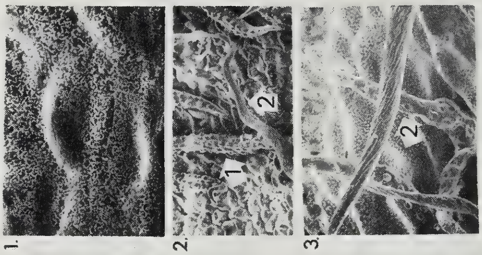
Erect, softly woody shrub up to 2 m tall; stem and older branches reddish brown and puckered with greyish lenticels (Fig. 5.3), branching mostly in the upper parts, greyish-white appressed strigulose when young but glabrous when mature. *Stipules* free, adnate to the base of the petiole, up to 5 mm long, subulate -setaceous, pubescent on the outside, glabrous inside. *Leaves* regular, odd pinnate, petiolate. *Leaflets* 16–18 mm long, 11–13 mm wide, 9–11 in number, suborbiculate to wide obovate, base obtuse, apex recurved mucronate, scurfy (Fig. 1), finely strigillose on both surfaces, two types of hairs (Figs 2–3), half-conduplicate. *Petiole* up to 2 mm long, petiolules shorter. *Inflorescences* axillary, racemose, densely many-flowered, pink, up to 12 cm long including a peduncle of 40–60 mm long, pubescent. *Flowers* 8–9 mm long, pink, each subtended by a 5–7 mm filiform, rapidly caducous bract, ebracteolate. *Calyx tube* 2 mm long, three times shorter than the calyx lobes; keel lobe 6,5 mm long, lateral lobes 6,0 mm long, vexillar lobes 4 mm long, tips flared, all linear, flattened, glabrous inside, villous outside. *Standard* 8–8,5 mm long, 4,2–4,7 mm wide, narrowly ovate, base narrowing into a flattened claw, auricles absent, apex acute, appendages absent. *Wing petals* 8 mm long, 2 mm wide, slightly auriculate, sculpturing basel and left central, of up to 10 thick lamellae. *Keel blades* 8 mm long, 2 mm wide, prominently pocketed, pocket 2 mm deep. *Pistil* 4,5 mm long, glabrous, 5–7-ovuled, sessile; style upcurved, height of curvature 1 mm; stigma capitate. *Vexillar stamen* free; anthers uniform, 1,5 mm long, strongly apiculate, dorsifixed, basal scales present and up to 0,5 mm long; staminal sheath 6 mm long. *Fruit* cylindrical (10) 15–25 mm long, 3 mm wide, dehiscent, blackish brown, septa 2 mm wide, barrel-shaped, separating the seeds. *Seeds* 2,25 mm wide and long, yellowish-green with blotches of purple of various intensities (Figs 4 & 5).

Indigofera superba is restricted to the mountains adjacent to Hermanus in the Caledon District (Fig. 6). This mountain fynbos endemic flowers in late summer and early autumn. Mature fruits have been found in early summer. It occurs between 100–300 m.

CAPE.—3419 (Caledon): near Nerina Pool (–AD), *Williams 2426* (NBG); near Vogelpool, Vogelgat (–AD), *Williams 2439, 2525* (K, NBG, PRE); near mountain hut on the Vogelgat Private Nature Reserve (–AD), *Stirton 8473* (PRE).

I have been unable to trace this species in any European of South African herbarium. It seems remarkable that such a distinctive and graceful plant should have escaped detection for so long. It was first collected in December 1977 by Dr Ion Williams. It grows quite commonly at the headwaters of a small stream that passed by the comfortable and peacefully isolated mountain hut that he has erected on his property. I am most grateful to Dr Williams for his generous hospitality and for drawing my attention to the possibility that this might be a new species.

Indigofera superba is not easy to place in Gillett's (1958) infrageneric classification of *Indigofera*. It shares the following characters with members of



FIGS 1–3.—1, scurfy abaxial surface of leaf of *Indigofera superba*, × 1200 (*Stirton* 8473). 2 & 3, abaxial surface of leaf of *Indigofera superba*, showing two types of hairs; 1, biramous warty hair curled at the tips and, 2, twisted hair with depressions. (2, × 240, 3, × 600). *Stirton* 8473.

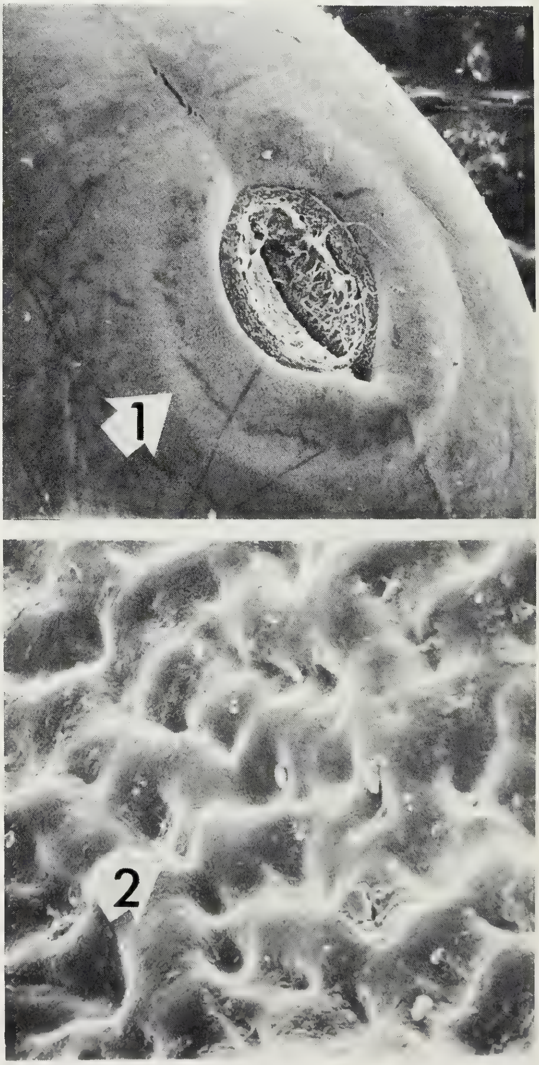


FIG. 4.—Seed of *Indigofera superba*. 1, hilar region, × 60; 2, surface pattern, × 650. *Stirton* 8473.

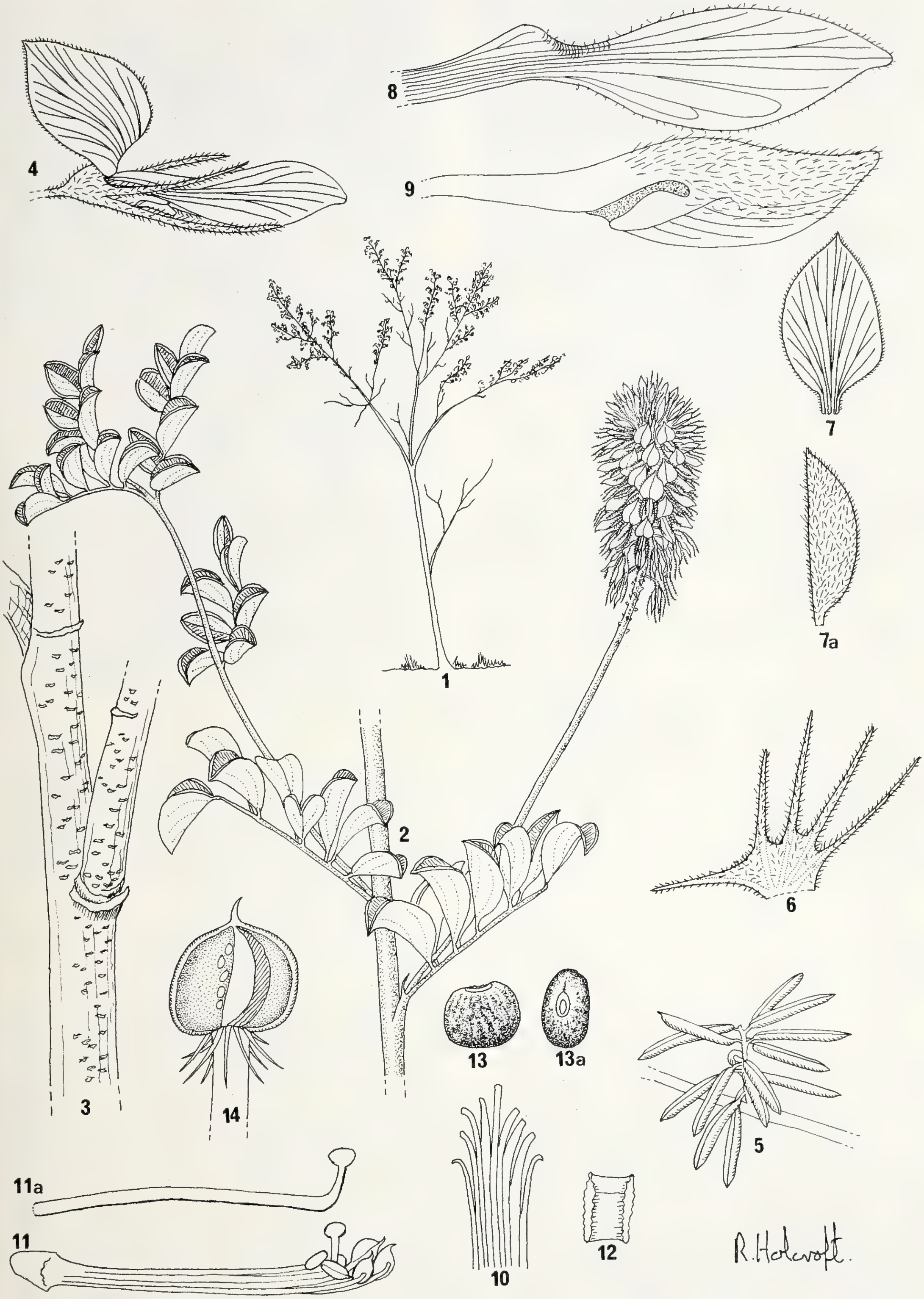


FIG. 5.—***Indigofera superba.*** 1, habit; 2, twig with inflorescence and leaves, × 1; 3, main stem, × 0,5; 4, flower, × 6; 5, infructescence, × 1; 6, calyx opened out, × 5; 7, standard opened out, × 4; 7a, standard closed, ×4; 8, wing petal, × 12; 9, keel petal, × 12; 10, apical part of staminal sheath flattened, × 10; 11, staminal sheath enclosing gynoecium, × 12; 11a, gynoecium, × 12; 12, seed partition, × 5; 13, lateral view of seed, × 5; 13a, ventral view of seed, × 5; 14, anther, × 40. (*Stirton* 8473 for fruits, seed, stem, habit; *Williams* 2439 for the rest.)

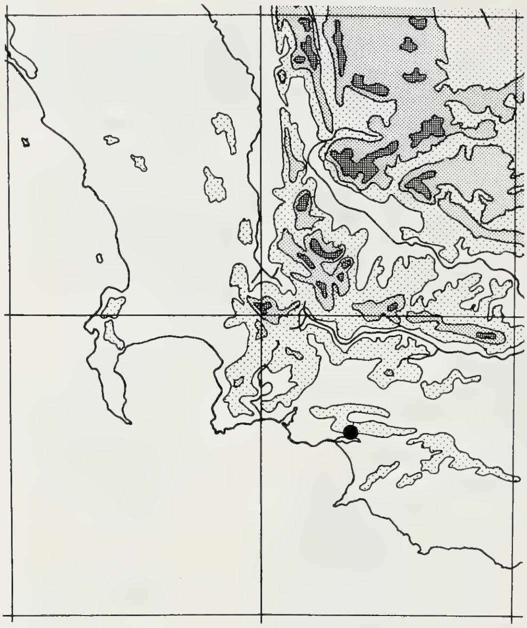


FIG. 6.—Known distribution of *Indigofera superba* in southern Africa.

sub-section *Psiloceratiae* Gillett: leaves pinnate; fruiting pedicel spreading; ovary and pod straight, glabrous; seeds 4 or more, well-separated. But it differs from the *Psiloceratiae* in that the rhachis is not prolonged beyond the opposite lateral leaflets and that the calyx is not shorter than the stamens. As Gillett has already pointed out the *Psiloceratiae* is perhaps an unnatural group. It does not seem to have a clearly identifiable sister species in southern Africa, although in some respects it approaches *I. velutina* E. Mey. I am grateful to Dr R. M. Polhill for his comments in this respect.

The description of this distinctive species perhaps underlies the poor state of our knowledge of the genus *Indigofera* in southern Africa. There are a few complex species in our region, but overall the species are very distinct and, when seen in the field, are unambiguously so.

Finally, I would like to thank Mr E. G. H. Oliver for doing the Latin diagnosis of the four new legumes described in these notes.

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C. H. STIRTON

A NEW SPECIES OF *OTHOLOBIUM* IN SOUTH AFRICA

The genus *Otholobium* C. H. Stirton was erected to accommodate some 40 species of southern and eastern African legumes placed previously in *Psoralea* L. sensu lato (Stirton, Advances in Legume Systematics 1: 337, 1981). Whilst engaged in a nomenclatural investigation of the genus, I came across the following undescribed species.

Otholobium pungens *C. H. Stirton*, sp. nov., *O. decumbenti* (Ait.) C. H. Stirton proximum, sed foliis subdigitatis, pungentibus, nitidis, obovatis, pellucido-glandulosis, calycis lobo carinali pungente, vexillo fere duplo majore diversum.

Frutex lignosus effusus, valde ramosus, caulibus veterioribus nigrescentibus prominenter subgriseo-lenticellatis. *Stipulae* conferruminatae, basi petioli adnatae, late oblique ovatae, margine ciliatae, extra basin versus tenuiter pubescentes, ceterum glabrae. *Folia* petiolata, subdigitata, trifoliolata. *Foliola* 8–10 mm longa, 2,5–3,0 mm lata, lateralia minora, costa excentrica, oblanceolata usque elliptica, basi cuneata, apice pungenti sed raro modice recurvo, nitida, glabra, nisi foliola juniora secus costam marginesque sparse pilosa, glandulis magnis pellucidis sphaericis immersis desuper visis prominentibus sparse obsita. *Inflorescentiae* axillares, 2–3-florae, apicem ramorum versus aggregatae, breviter pedunculatae, bractea obovata dentata 2,5–4,0 mm longa suffultae. *Flores* 9–11 mm longi, 4–5 mm lati, violacei, ebracteolati, bractea lineari 4 mm longa suffulti. *Calycis* dentes tubo longiores, prominenter 3-costati, lobo carinali late ovato glanduloso pungenti excepto omnes lanceolati, lobis vexillaribus haud connatis. *Petala alaria* carina multo longiora. *Ovarium* sessile, 1-ovulatum, glandulis clavatis recurvatis sparse obsitum, stigmate oblique penicillato. *Fructus* et semina ignota.

TYPE.—Cape, 3420 (Bredasdorp): Potberg North (–BC), *Acocks 22835* (K, holo.!). Fig. 7.

Spreading, decumbent, much-branched woody shrub; old branches blackish but puckered with distinctive rectangular bands of grey-white lenticels, glabrous; young branches green, sparsely pilose, finely ribbed. *Stipules* fused, adnate to the base of the petiole, 3–4 mm long, 1,5–2,0 mm wide, broadly and obliquely ovate, acute, striate, glabrous inside, sparingly white pubescent outside towards the base, otherwise glabrous, margins ciliate. *Leaves* trifoliolate, subdigitate, petiolate. *Leaflets* 8–10 mm long, 2,5–3,0 mm wide, oblanceolate, rarely elliptic, base cuneate, apex sharply pungent, rarely recurved, shiny, glabrous except for younger leaves which are sparingly hairy along the midrib and margins, sparingly covered in large spherical internal pellucid glands prominent when seen from above; lateral leaflets smaller, excentric. *Petiole* 2,5–4,0 mm long, petiolules very short. *Inflorescences* axillary, 3- rarely 2-flowered, clustered towards the

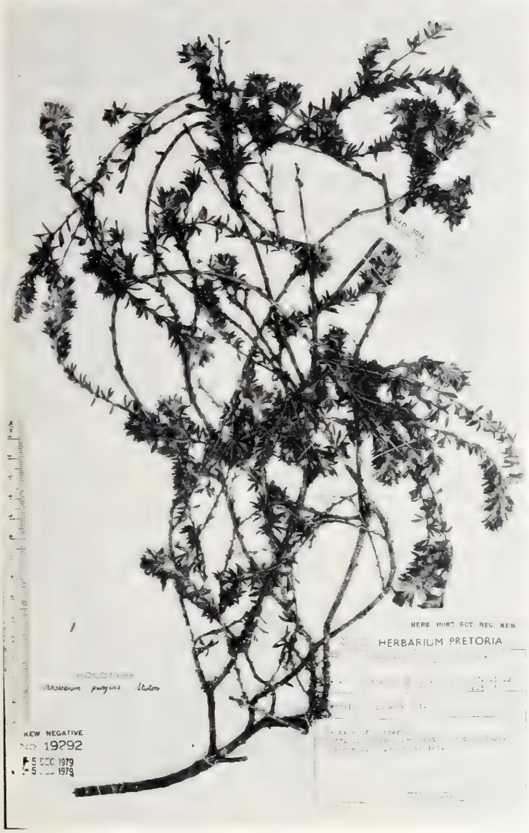

FIG. 7.—*Otholobium pungens*, holotype in K, × 0,3. *Acocks* 22835.

ends of branches, shortly pedunculate, each inflorescence subtended by a 2,5–4,0 mm long, glabrous toothed, obovate bract with ciliate margins. *Flowers* 9–11 mm long, 4–5 mm wide, light violet, each subtended by a 4 mm long linear bract, ebracteolate. *Calyx* tube 3 mm long, lobes 5 mm long, each tooth prominently 3-ribbed, all lanceolate except the broadly ovate, glandular and pungent keel lobe, hairy along the ribs and on the tube, inner face of teeth finely pubescent. *Standard* 12 mm long, 11 mm wide, broadly-obovate, auriculate, appendages absent, claw 3 mm long, apex emarginate, only sides of the standard reflexed. *Wing petals* 11 mm long, 4 mm wide, cultrate, auriculate, sculpturing upper basal consisting of ± 9 recurved lamellae. *Keel* 7 mm long, 2 mm wide, purple-tipped, shorter than wing petals. *Pistil* 5,5 mm long, glabrous; ovary 3 mm long, l-ovuled, sessile, sparsely covered with recurved clubshaped glands; style gently upcurved, swollen at point of curvature, height of curvature 2,5 mm; stigma oblique, penicillate. *Vexillar stamen* free, anthers uniform, alternately basifixed and medifixed on long and short filaments respectively. *Fruit* and seed unknown. Fig. 8.

Otholobium pungens appears to be restricted to the transition zone between Mountain Fynbos and Renosterbosveld in the vicinity of Potberg. It occurs commonly in rocky places along the gentle lower slopes of the Potberg.

CAPE.—3420 (Bredasdorp): north of Potberg (–BC), *Acocks* 22835 (PRE; K); *Taylor 7200* (PRE, K, STE); west base of the Potberg (–BC), *Pillans s.n.* (BOL; K).

This distinctive but rarely collected species stands out from all other species of *Otholobium* by its sharply pointed leaves and lower calyx tooth; hence the specific epithet *pungens*.

C. H. STIRTON

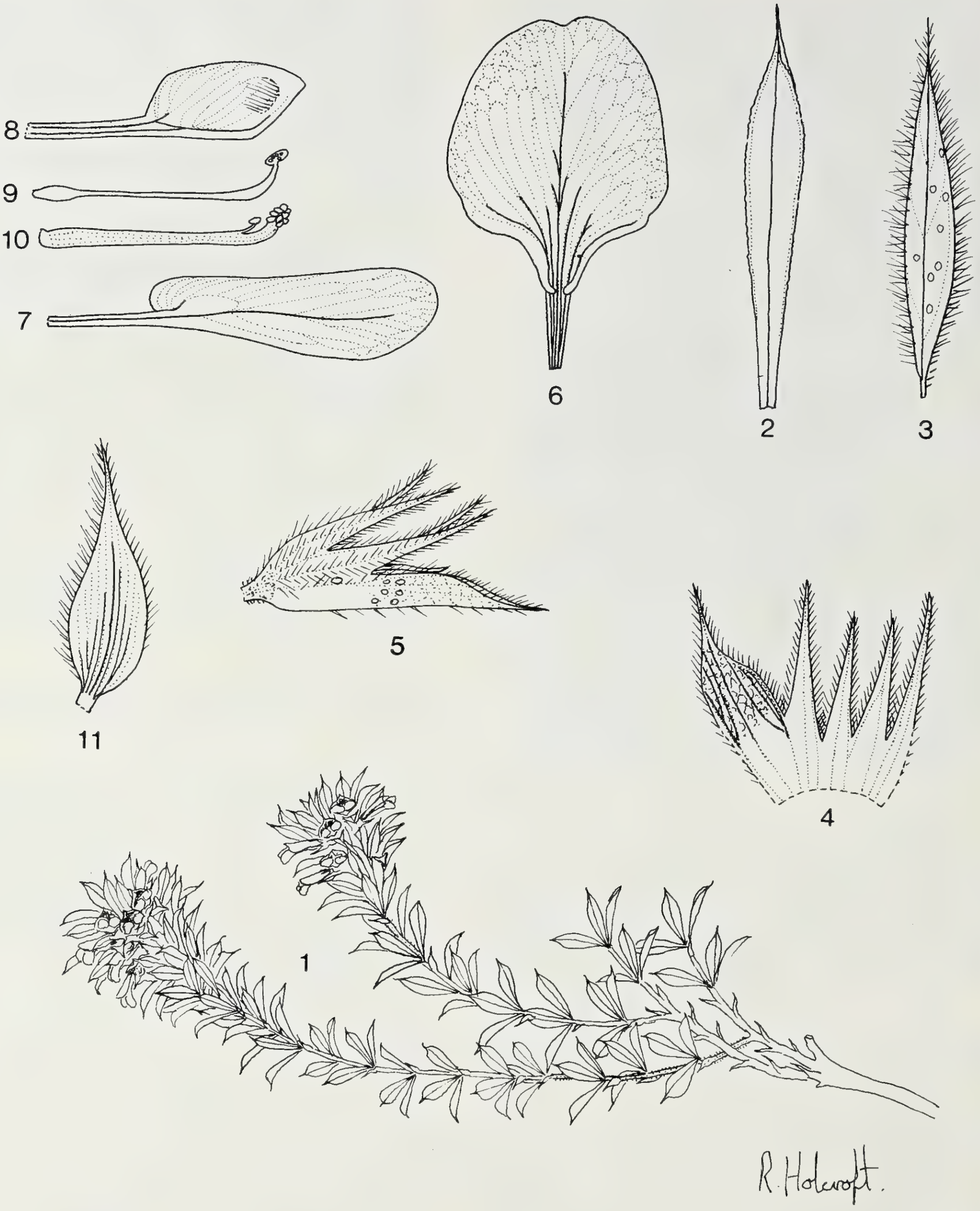

Fig. 8.—*Otholobium pungens.* 1, habit × 1; 2, terminal leaflet, × 6; 3, lateral leaflet, × 6; 4; calyx opened out, × 4; 5, calyx closed, × 5; 6, standard opened out, × 6; 7, wing petal, × 6; 8, keel petal, × 6; 9, gynoecium, × 6; 10, androecium, × 6; 11, flower bract, × 10.

A NEW SPECIES OF *RAFNIA* FROM THE CAPE

Rafnia crispa *C. H. Stirton,* sp. nov. (Sect. *Eu-rafnia,* subsect. *Angustifolia* Harv.) *R. Lancea* (Thunb.) DC. proxima a qua vexillo anguste unguiculato late ovato, carina acute rostrata, calyci dissimili et margine folii crispato cartilagineo differt.

Planta erecta herbacea perennis ad 40 cm alta glabra, caudice lignoso exorienti. *Folia* simplicia 50–65 mm longa, 15–17 mm lata, vetiora minora, denum bracteae apicibus florentibus fere similia elliptica, margine crispato cartilagineo. *Inflorescentia* axillares, flore uno, terminaliter surculis longis aggregata. *Flores* 13–15 mm longi, flavi. *Calyx* 12 mm longus, dentibus tubo 7 mm longo angustioribus, dente carinae angustissimo setaceo dentibus

vexilli lateralibusque triangulare-acuminatis et conjunctioribus. *Vexillum* 14–15 mm longum, 14 mm latum, latissime ovatum, emarginatum, breviter unguiculatum. *Alae* 15 mm longae, 8 mm latae, obovatae, carinam superantes. *Laminae carinae* 14 mm longae, 7 mm latae ad partem maximam, apice rostrato, acute sursum curvato. *Vagina* staminealis 14 mm longa, antheris 5 parvis 1 mm longis dorsifixis et antheris 4, 2,25 mm longis basifixis alternantibus, anthera carinae intermedia. *Pistillum* 13 mm longum; stylo filiformi, acute sursum curvato; stigma capitata, subtiliter fimbriata.

TYPE. — 3319 (Worcester): Kluitjeskraal (–AC), *Stirton 8439* (PRE, holo!).

Erect herbaceous perennial up to 40 cm high, glabrous, arising from a woody rootstock. *Leaves* simple, alternate, sessile, estipulate 50–65 mm long, 15–17 mm wide, becoming smaller and eventually almost bractlike at the flowering apices, elliptic, apex attenuate, base decurrent; brochidodromous, primary vein moderately thick, straight, secondary veins diverging from primary vein at ≤ 45°, divergence angle nearly uniform, course abruptly curved, joining secondary at an obtuse angle, margin crispate, cartilaginous. *Inflorescences* axillary, single flowered, clustered terminally on long shoots. *Flowers* 13–15 mm long, bright yellow, each subtended by small bracts; bracteoles 2 mm long. *Pedicel* 1–2 mm long. *Peduncle* 13—15 mm long. *Calyx* 12 mm long, teeth shorter than the 7 mm long tube, keel tooth shortest, setaceous, vexillar and lateral teeth triangular — acuminate and more united. *Standard* 14–15 mm long, 14 mm wide, very

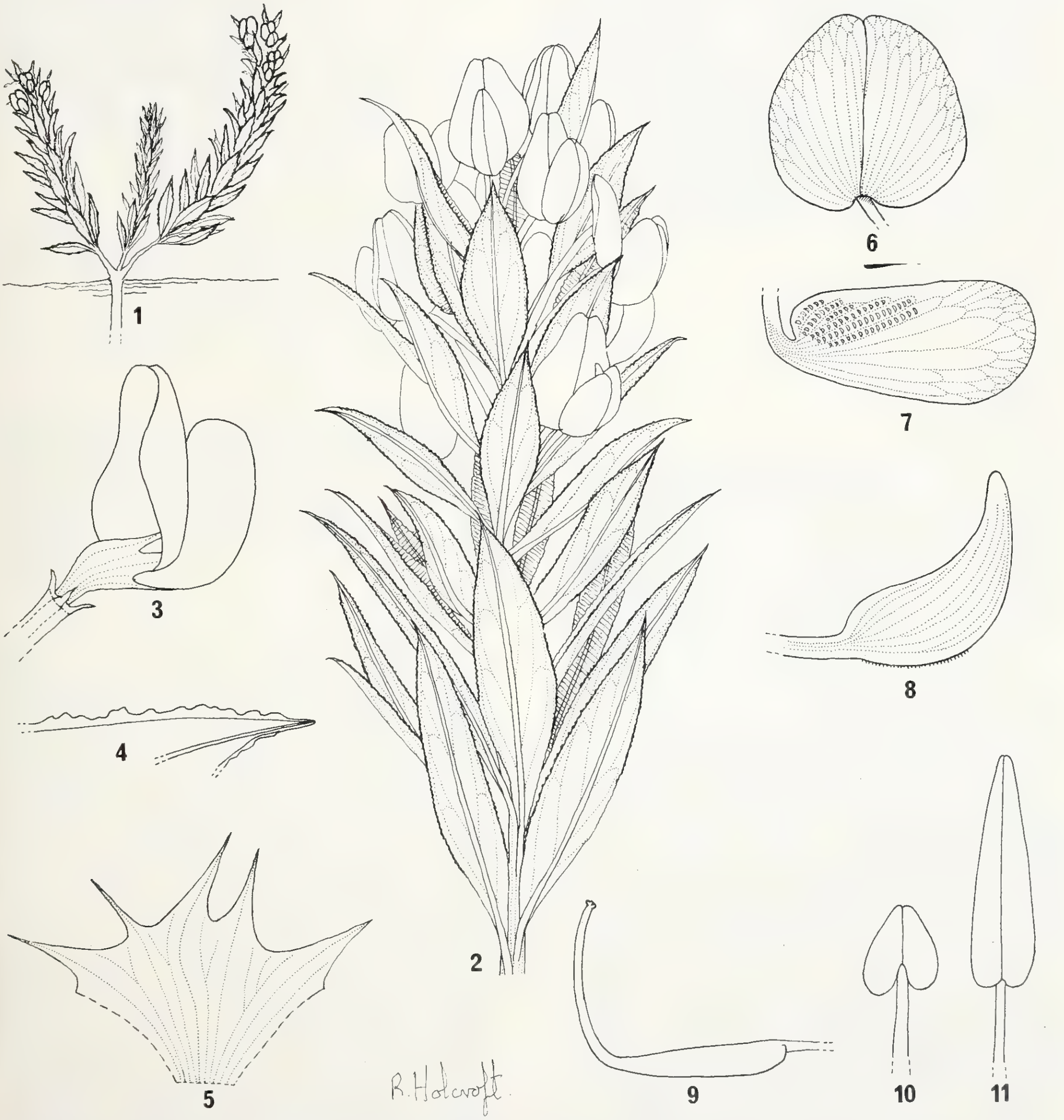

FIG. 9.—*Rafnia crispa*. 1, habit; 2, terminal inflorescence, × 1;3, flower, × 2; 4, leaf margin, × 2; 5, calyx opened out, × 3; 6, standard opened out, × 2; 7, wing petal showing intracostal lunulae, × 3; 8, keel petal with hairs along base, × 3; 9, gynoecium, × 3; 10, versatile anther on shorter filament, ×18; 11, basi-fixed anther on longer filament, × 18.

wide ovate, emarginate, shortly clawed, auricles and appendages absent. *Wings* 15 mm long, 8 mm wide, obovate, exceeding the keel; sculpturing present, upper basal and left central, lunulate, each of 5–6 rows comprising 15–25 intercostal lunulae. *Keel blades* fused, 14 mm long, 7 mm wide at maximum, claw 5 mm long, apex rostrate, sharply upcurved, height of curvature 7 mm. *Staminal sheath* 14 mm long, split on upper side, with five small 1 mm long dorsifixed anthers alternating with four 2,25 mm long basifixed anthers, carinal anther intermediate. *Gynoecium* 13 mm long, style filiform, sharply upcurving, height of curvature 9 mm high, stigma capitate, finely fringed, seeds and fruits unknown (one ovary contained two ovules). Fig. 9.

Rafnia crispa is a rare species of open flat well-drained sandy sites. I encountered only a few plants in the Kluitjeskraal Forestry area (Fig. 10) but a wider search may reveal a more extensive population. This species was found in full flower in early December.

R. crispa a clearly related to *R. lancea* (Thunb.) DC., which also grows in the region but among sandy-rocky sites in the mountains to the west of the Tulbagh flats. They seem to be vicariant species.

The specific epithet *crispa* refers to the distinctive crisped leaf margins.

C. H. STIRTON

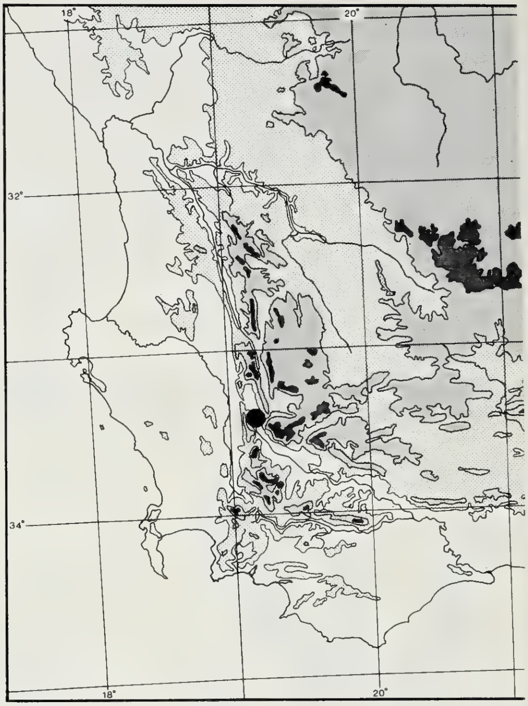

FIG. 10.—Known distribution of *Rafnia crispa* in South Africa.

A NEW SPECIES OF *RHYNCHOSIA* FROM VENDA

Rhynchosia vendae *C. H. Stirton*, sp. nov., affinitate incerta.

Planta perennis volubilis caulibus teretibus, pilis dense appressis tenuibus tectis et pilis patentibus glandulosis inter eos dispersis. *Stipulae* appressae, subulatae, celeriter caducae. *Foliola* 3, 45–87 mm longa, 36–65 mm lata, lateralia minora, valide gibbosa, supra subtiliter pubescentia glandibus paucis dispersis, inferne grosse pubescentia pilis in venas angulatis aliter patentibus, glandibus multis croceis in intervenia dispersis; nervatura in superficiebus ambabus prominenti. *Inflorescentiae* 1–2, axillares, racemosae, laxae, 15–25 floribus binatim spiraliter insertis. *Flores* 16–18 mm longi, flavo-brunnei, quoque parvi florum bractea ovata 4–5 mm longa celeriter caduca, subtento. *Calyx* subtiliter pubescens; tubo 3,5–4,0 mm longo; lobis anguste triangularibus; lobis vexillaribus per plus minusve ⅞ longitudinis conjunctis. *Vexillum* 18 mm longum, 13 mm latum, late obovatum, apice rotundato, appendiculatis bilobatis, auriculis liberum. *Alae* 13 mm longae, 4 mm latae flavae, dimidiae longitudinis carinae, auriculatae parum saccatae. *Petala carinae* 20 mm longa, 8 mm lata, marsupio extus ad basim. *Pistillum* 4,5 mm longum, dense pubescente. *Fructus* 35–40 mm longi, oblongo-falcati, angustiores ad basim, apice deorsum curvati.

TYPE. — Cape, 2230 (Messina): Punda Maria (–CA), *Van der Schijff 3596* (PRE, holo!).

Perennial twiner with terete stems, densely clothed with thin appressed soft hairs and with patent glandular-based hairs scattered among them. *Stipules* appressed, up to 4 mm long, 3 mm wide at the base, subulate, rapidly caducous, densely glandular outside, sparsely hairy inside. *Leaflets* 3, 45–87 mm long, 36–65 mm wide; laterals smaller, strongly gibbous with width ratio 2,2–2,4; apex acute, base truncate to broadly cuneate; finely pubescent above with a few scattered glands, coarsely pubescent below with hairs angled on the veins, otherwise patent, and with numerous small orange-coloured glands scattered in the intervenal areas; nervation prominent and raised on both surfaces. *Petiole* 25–60 mm long. *Petiolules* 2–3 mm long, canaliculate, stipellate. *Inflorescences* 1–2, axillary, racemose, laxly 15–25-flowered, with flowers borne in pairs, inserted spirally, flowers 16–18 mm long; yellowish-brown; each pair subtended by a 4–5 mm long, ovate, rapidly caducous bract; ebracteolate; pedicels 7–10 mm long. *Calyx* finely pubescent on the outside and on the inner face of the teeth; glandular on the outside only; tube 3,5–4,0 mm long; lobes narrowly triangular, keel lobe the longest, 8–10 mm long, the other lobes all 7,0–8,5 mm long; vexillar lobes joined for ± ⅞ of their length. *Standard* 18 mm long, 13 mm wide, broadly obovate, narrowing into an auriculate 3 mm long claw; apex rounded; appendages present, bilobed, 1,5 mm above and free from auricles. *Wings* 13 mm long, 4 mm wide, yellow, half the length of the keel, auriculate, slightly pouched. *Keel petals* 20 mm long with 5 mm long claw, 8 mm wide, pocket present on the outside towards the

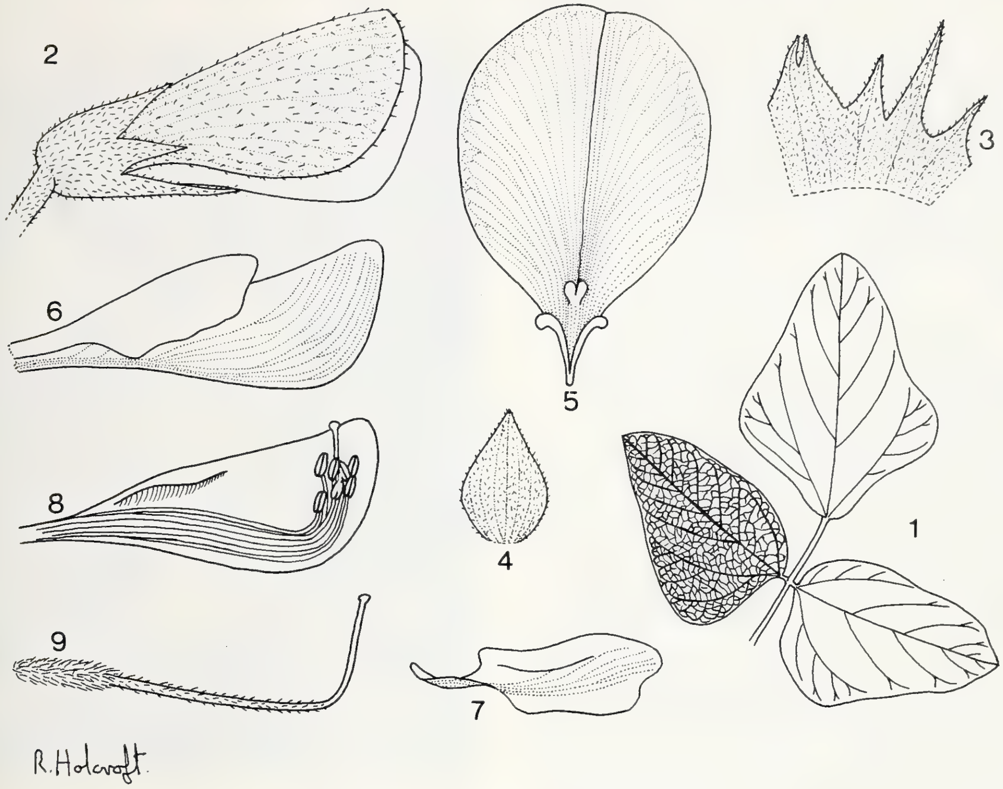

FIG. 11.—*Rhynchosia vendae*. 1, trifoliolate leaf, × 0,5; 2, flower, × 3; 3, calyx opened out, × 3; 4, flower bract, × 3; 5, standard opened out, front face, × 3; 6, wing petal interlocking with keel petal, × 3; 7, wing petal, × 3; 8, position of pistil and gynoecium within the keel, × 3; 9, pistil, × 3.

base, 1–1,5 mm deep, auricles absent. *Stamens* diadelphous, sheath split adaxially; anthers monomorphic, anthers alternately basifixed and dorsifixed, 1–1,3 mm long. *Pistil* bi-ovulate, 4,5 mm long, densely pubescent; style bent, height of curvature 6 mm, pubescent to the point of flexure. *Fruits* 35–40 mm long, oblong falcate, narrowed towards the base, recurving downwards at the tip. *Seeds* unknown. Fig. 11.

Rhynchosia vendae appears to be restricted to Acocks's veld type 8, the North-eastern Mountain Sourveld (Fig. 12). Within its range, it occupies diverse habitats such as wooded watercourses, sandveld and rocky outcrops. Flowering takes place from December to March, with fruiting concentrated in March and April.

VENDA.—2230 (Messina): 11 km north-west of Punda Milia (–DB), *Codd 6533* (PRE); 35 km north of Sibasa on the road to Rambunda (–DC), *Codd 6897* (PRE). 2231 (Pafuri): south east of Klopperfontein near the Mozambique border (–CA), *Van der Schijff 2964* (PRE); Punda Milia (–CA), *Van der Schijff 3355, 3596* (PRE)

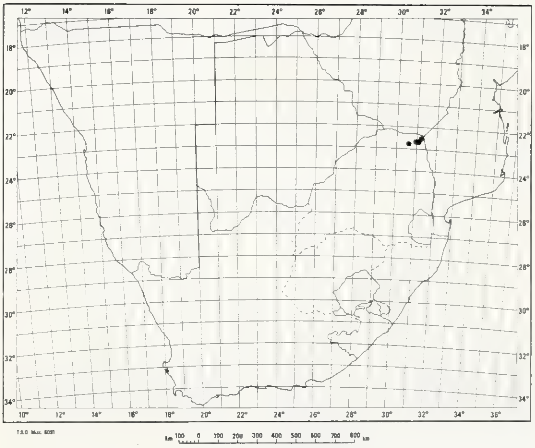

FIG. 12.—Known distributions of *Rhynchosia vendae* in Southern Africa.

The Vendan name for *R. vendae* is 'lufoko', meaning 'light dust'. Some Vendans use the perennial rootstocks to make a remedy for coughs. The specific epithet *"vendae"* is given in honour of the Vendan people.

C. H. STIRTON

IRIDACEAE

A NEW SPECIES OF *GLADIOLUS*

Gladiolus cataractarum *Oberm.*, sp. nov., *G. microcarpo* affinis, sed planta glabra bracteis majoribus pedunculum et rhachim occultans differt.

Planta glabra robusta c. 700 mm alta. *Cormus* globosus parvus c. 30 mm diam. *Folia* c. 6, late ensiformia longe vaginantes acuminata ad 600 × 45 mm mollia. *Spica* erecta secunda c. 6–16-flora; bracteae longe vaginantes, pedunculum et rhachim occultans attenuatae c. 70 mm longae; bracteolae interiores c. 40–50 mm longae tubus perianthii cingentes. *Perianthium* c. 90 mm longum roseum; tubus strictus curvatus c. 40 mm longus; lobi superiores anguste obovati c. 45 mm longi 15 mm lati; lobi inferiores parum minori recurvati. *Stamina* et gynoecium typica. *Capsula* non vidi.

TYPE. — Transvaal, 2530 (Lydenburg): Lunsklip, on farm Waterval near Dullstroom (–AD) in wet grassy areas, *J. Krijt in PRE 58472* (PRE, holo.), flowering Feb. 1981.

Tall, glabrous plants c. 700 mm tall when in flower. *Corm* c. 30 mm in diam, with old corms at the base. *Leaves* c. 6, broadly ensiform, acuminate, up to 600 × 45 mm, long-sheathing below, finely ribbed, thin. *Spike* secund, c. 6–16-flowered, peduncle and rhachis hidden by the long leafbases and sheathing bracts, which are attenuated above and c. 70 mm long; *Perianth* c. 90 mm long, rose-pink, the 3 upper lobes with a faint thin red medium stripe, the 3 lower with a distinct thin red stripe; perianth-tube curved, narrow, c. 40 mm long, expanding above into a spreading limb; 3 upper lobes narrowly obovate, c. 45 mm long, 15 mm wide; lower slightly narrower, curved downwards; stamens and gynoecium typical. *Capsule* not seen. Fig. 13.

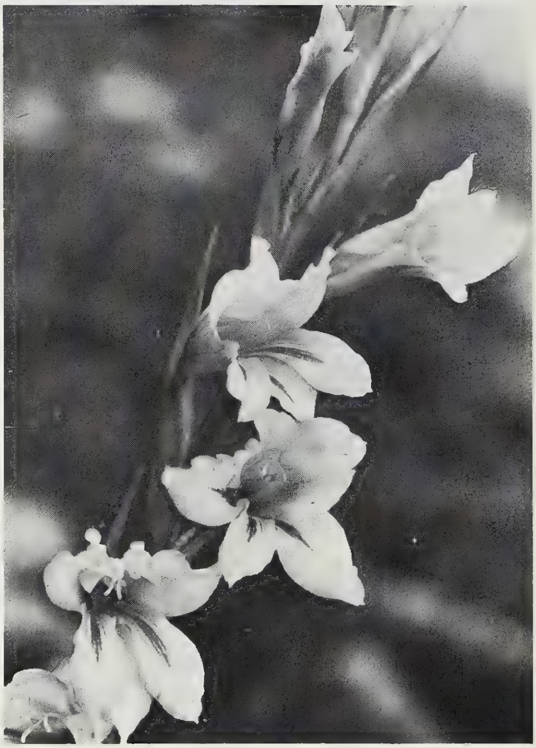

FIG. 13.—*Gladiolus cataractarum* at the type locality. March 1981. Photo. S. P. Fourie (Transvaal Nature Conservation Department).

This beautiful species known so far only from the type locality, differs from typical *G. microcarpus* Lewis and its subspecies *italaense* Oberm. in being completely glabrous, in the large imbricate floral bracts and the larger leaves and flowers. From *G. varius* Bol. f. it can be easily distinguished by its very broad leaves and the large green floral bracts.

A. A. OBERMEYER

LILIACEAE

RHADAMANTHOPSIS CHANGED TO *DRIMIOIDES*

In Bothalia 13: 137 (1980) a new subgenus in the genus *Rhadamanthus* was given the name *Rhadamanthopsis* Oberm. However, according to the ICBN, Article 21.3, this name must be rejected. The name *Drimioides* Oberm. is therefore substituted for this subgenus: although the termination *-oides* is used, it is not added to the name of the genus to which the subgenus belongs.

A. A. OBERMEYER

MALPIGHIACEAE

NAME CHANGES AND CHANGES OF RANK IN *TRIASPIS* BURCH.

The genus *Triaspis* Burch. [Trav. S. Afr. 2: 280 (1824)] has until now been considered to have eight species and a varying number of varieties in southern Africa. As a result of work done for a revision to be published in the Flora of Southern Africa, the number of species has been reduced to two, with two subspecies.

T. nelsonii Oliv. (1833) has been reduced to a subspecies of *T. hypericoides* (DC.) Burch. (1824). *T. hypericoides* subsp. *nelsonii* differs in both leaf shape and geographical range from the typical *T. hypericoides,* but this difference is considered to warrant only subspecific rank.

T. nelsonii subsp. *canescens* (Engl.) Launert becomes *T. hypericoides* subsp. *canescens.* Only the type and one other collection have been seen by the author, who has therefore preferred to be conservative and retain the subspecies as a distinct entity. The leaves are smaller than is typical of *T. hypericoides* and the leaves remain densely pilose even at maturity. It also appears to be geographically partially distinct, being from Mozambique and the Kruger National Park (subsp. *nelsonii* is also found in these areas).

Only basionyms and species formerly regarded as distinct are given in synonymy. Full synonomy and descriptions will be given in F.S.A.

Key to species

Wing on carpel 1,2–2,0 times longer than wide, 10–25 mm in width; leaf 0,7–1,6 times longer than wide; petiole (2–) 4–16 (–20) mm long .... 1. *T. glaucophylla*

Wing on carpel 0,8–1,3 times as long as wide, 25–40 mm in width; leaf (1,0–) 1,2–3,0 (–6,5) times longer than wide petiole 1–5 (–7) mm long .... 2. *T. hypericoides*

1. **Triaspis glaucophylla** *Engl.* in Bot. Jb. 36: 249 (May, 1905). Type: Transvaal, N.W. of Lydenburg, by big waterfall, *Wilms 144* (B?).

T. leendertziae Burtt Davy, Fl. Transv. 1: 51 (1926), 2: 286 (1932). Type: Transvaal, Potgietersrust, *Leendertz 1962* (K. holo.!; BOL!).

2. **Triaspis hypericoides** (*DC.*) *Burch.* Trav. S. Afr. 2: 280, 290 (Jan.–June, 1824) — Syntypes: Cape, Kosi Fountain, *Burchell 2531* (K, lecto.!); Cape, in a walk to, and on a black rocky hill under, the Kamhanni Mnts (Kuruman Hills), *Burchell 2486* (K).

Key to the subspecies

Leaf lamina canescent at all stages .... (c) subsp. *canescens*
Leaf lamina soon becoming glabrescent (hairs sometimes remaining on midrib beneath and on margins):
  Leaves 3,0–6,5 times longer than wide; occurring in Botswana and northern Cape........... (a) subsp. *hypericoides*
  Leaves 1,0–3,0 times as long as wide, occurring in South West Africa/Namibia and Transvaal .... (b) subsp. *nelsonii*

(a) subsp. **hypericoides**

Hiraea hypericoides DC., Prodr. 1: 585 (Jan., 1824).

(b) subsp. **nelsonii** (*Oliv.*) *Immelman* stat. nov.

T. nelsonii Oliv., in Hooker's Icon. Pl. 15, 14: t. 1418 (1833). Type: Transvaal, Pretoria *Nelson* 511 (K. holo.; PRE!).

T. hypericoides var. *subsessilis* Burtt Davy, Fl. Transv. 1: 51 (1926), 2: 286 (1932). Type: Transvaal, *Todd* 26 (K, holo.!).

T. thorncroftii Burtt Davy, Fl. Transv. 1: 51 (1926), 2: 286 (1932). Type: Transvaal, Tzaneen, *Rogers* 12572 (K, holo.!; BOL!; photo. at PRE!).

T. ternata Greenway & Burtt Davy, Fl. Transv. 1: 51 (1926), 2: 286 (1932). Type: Transvaal, Komatipoort, *Rogers* 22172 (K, holo.; BOL!).

T. ovata Bremek. in Ann. Transv. Mus. 15: 245 (1933). Type: Transvaal, Pietersburg, Olifantsrivier, Molsgat, *Bremekamp & Schweikerdt* 450 (PRE!; PRU).

(c) subsp. **canescens** (*Engl.*) *Immelman* comb. nov.

T. canescens Engl. in Bot. Jb. 36: 249 (1905). *T. nelsonii* subsp. *canescens* (Engl.) Launert in Bolm Soc. broteriana sér 2, 35: 32 (1961). Type: Mozambique, Ressano Garcia, *Schlechter* 11827 (K, lecto; GRA!; B†).

K. IMMELMAN

NYCTAGINACEAE

THE IDENTITY OF *BOERHAAVIA PTEROCARPA* IN SOUTH AFRICA

The correct name of the plants referred to as *Boerhaavia pterocarpa* S. Wats. in South Africa is *B. cordobensis* Kuntze. *B. pterocarpa* was first recorded as a weed in South Africa by Codd in 1966 (Bothalia 9: 113–121). In discussing its identity he commented that the specimens available to him for study were 'an excellent match of the type of *B. cordobensis* Kuntze, which comes from the Argentine'. He also noted, however, that ' . . . a specimen of *Leistner* 1084 was sent to the Gray Herbarium of Harvard University, where it was reported to be an almost perfect match of the type of *B. pterocarpa* S. Wats.'. It was the latter, incorrect assessment which led him to accept the name *B. pterocarpa* S. Wats. (Proc. Am. Acad. 17: 376, 1882) over *B. cordobensis* Kuntze (Rev. Gen. 3,2: 264, 1898). However, as these two names refer to two distinct taxa it becomes necessary to call the South African material *B. cordobensis.*

An easily detected difference between *B. pterocarpa* and *B. cordobensis* lies in the side walls of the fruit. In *B. pterocarpa* the side walls of the fruit are corrugated, evident from even an early stage of development, whereas in *B. cordobensis* they are smooth. B. pterocarpa does not occur in

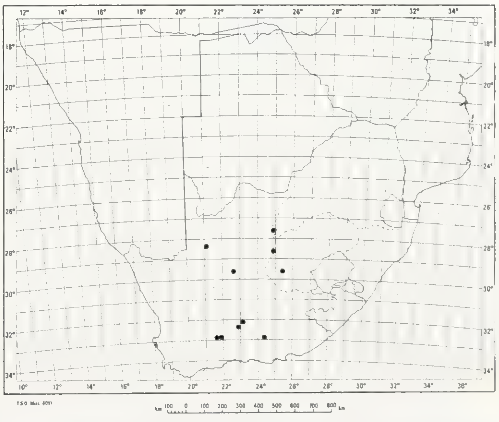

FIG. 14.—Known distribution of *Boerhaavia cordobensis* in South Africa.

South Africa. The distribution of *B. cordobensis* is given in Fig. 14.

I am indebted to Mr R. D. Meikle, Royal Botanic Gardens, Kew, for comparing South African material of *B. cordobensis* against the type of *B. pterocarpa,* kindly loaned to me by Harvard University, and to Dr H. F. Glen for sending me excellent colour photographs of the type material.

C. H. STIRTON

ROSACEAE

THE CORRECT NAME FOR PLANTS CALLED *AGRIMONIA ODORATA* IN SOUTHERN AFRICA

The correct name of the plants referred to as *Agrimonia odorata* Mill. in South Africa is *Agrimonia procera* Wallr. (Erst, Beitr. Fl. Hercyn, 203 (1840) = *A. odorata* auct., non Mill., *A. eupatoria* L. var. βL.).

Agrimonia procera is superficially similar to *A. eupatoria* which I suspect also occurs in South Africa. The two species can be separated as follows:

Mature hypanthium grooved for ½ its length, lowest bristles distinctly deflexed; stems clothed only with long eglandular hairs .... *A. procera*
Mature hypanthium grooved for at least ¾ of its length, lowest bristles rarely deflexed, if so only slightly; stems clothed with both long and short eglandular hairs .... *A. eupatoria*

C. H. STIRTON

SCROPHULARIACEAE

NOTES ON THE GENUS *APTOSIMUM*

The acceptance of the proposal to conserve *Aptosimum* Burch. ex Benth. against *Ohlendorffia* Lehm. (see Taxon 25: 190, 1976) means that the generic name for the well-known Karoo Violet is retained, but that *depressum* may not be used as the specific epithet. Certain other small changes are noted below.

Aptosimum *Burch. ex Benth.* in Bot. Reg. new ser. 9: t. 1882 (1836), nom. cons. Type species: *A. depressum* Burch. ex Benth.

Aptosimum Burch., Trav. 1: 129 (1822), non rite publ.
Ohlendorffia Lehm., Del. Sem. Hort. Hamburg bot. 7 (1835).

A. procumbens *(Lehm.) Steud.,* Nom. Bot. edn 2, 1: 114 (1841). Type: Cape, Hermanskraal (now Fort Brown), ex hort. Hamburg, *Ecklon* (no herbarium specimen can be traced but Bot. Reg. t. 1882 was prepared from the cultivated plant and may be regarded as representative).

Ohlendorffia procumbens Lehm., l.c.
Ruellia depressa L.f., Suppl. 290 (1781); Thunb., Prodr. 2: 104 (1800), Fl. Cap. edn Schult. 479 (1823). Type: Cape, *Thunberg* s.n. (UPS).
A. depressum Burch., Trav. 1: 260 (1822), nom. nud.
A. depressum Burch., ex Benth. in Bot. Reg. new ser. 9: t. 1882 (1836), nom. illegit; Dyer & Milne-Redh. in Kew Bull. 1934: 265 (1934). Iconotype: Bot. Reg. t. 1822 (no herbarium specimen found in K or CGE).

var. **elongatum** *(Hiern) Codd,* comb. nov.

A. depressum var. *elongatum* Hiern in Fl. Cap. 4,2: 131 (1904). Lectotype: Transvaal, Pienaars River, *Schlechter* 4223 (K, lecto.).
A. elongatum Engl. in Bot. Jb. 10: 249 (1888); Hemsl. & Skan in Fl. Trop. Afr. 4,2: 273 (1906). Type: Cape, Barkly West, *Marloth* 831.

A. indivisum *Burch. ex Benth.* sub Bot. Reg. new ser. 9: t. 1882 (1836). Lectotype: Karoo, *Drège* 620 (K).

A. indivisum Burch., Trav. 1: 219 (1822), nom. illegit.

Burchell, in his Travels in Southern Africa 1: 129 (1822), published the name *Aptosimum* without a description, giving only a short explanatory note on the derivation of the name from the Greek words *a,* not, and *ptosimos,* deciduous, in reference to the capsules remaining on the stems long after the seeds are shed. This short note might, by some, be regarded as adequate for the requirements of the Code, but the consensus of opinion, when the subject was submitted to the nomenclatural committee, was that it was insufficient.

The fact that Burchell, on the same page, described the species *A. indivisum* cannot be adduced as a generico-specific description (Art. 42) because on p. 308 he described a second species, *A. abietinum* Burch., while on p. 260 he listed *A. depressum* without description or citation of a basionym. It may be noted that *A. abietinum* is now included in *A. spinescens* (Thunb.) Web.

The names and author citations of all the other species of *Aptosimum* are not affected.

Ohlendorffia procumbens Lehm., Del. Sem. Hort. Hamburg bot. 7 (1835), was based on living plants raised in the Hamburg Botanic Garden (where Ecklon stayed from 1833 to 1837) from seed collected by Ecklon at 'Herrmans-kraal' on the Great Fish River. Hermanskraal is now Fort Brown, about 22 km north of Grahamstown. Lehmann named the genus after a promising young botanist, C. F. Ohlendorff of Holstein, who had died on the Danish island of St Croix in the West Indies. He also supplied a painting and specimen to John Lindley, who published the illustration, with a description of the species and notes on the genera *Aptosimum* and *Peliostomum* drawn up by Bentham, in Bot. Reg. t. 1882 (1836).

Bentham realized that Lehmann's plant was conspecific with the one listed by Burchell as *Aptosimum depressum,* but saw no reason to reject Burchell's name and presented the synonymy as follows:

Aptosimum depressum *Burch.*
  Ruellia depressa Thunb.?
  Ohlendorffia procumbens Lehm.

The Thunb. citation refers to *Ruellia depressa* L. f., Suppl. 290 (1781), based on a Thunberg specimen collected at the Cape. Thunberg took up the name in his Prodr. 2: 104 (1800) and Fl. Cap. edn Schult. 479 (1823). Dyer & Milne-Redhead examined a specimen on loan from Uppsala of the above Thunberg gathering and reported that it agrees well with the Bot. Reg. illustration and with *Burchell* 1354, listed by Burchell as *Aptosimum depressum.* They concluded that the correct citation for the species should be *Aptosimum depressum* (L. f.) Burch., ex Benth. However, they overlooked the significance of the question mark which Bentham added after *Ruellia depressa* Thunb. This indicated that Bentham was not sure of the identity of *Ruellia depressa* so his use of the epithet *depressum* cannot be regarded as being a transfer from *Ruellia.* Nor is there any indication that Burchell was taking up the Linn. fil. epithet when he published the nomen nudum *A. depressum.* Because Bentham expressed uncertainty regarding the identity of *'Ruellia depressa* Thunb.', he should have taken up Lehmann's epithet *procumbens.* This means that *Aptosimum depressum* Burch. ex Benth. is a superfluous name and therefore illegitimate, so that the Linn. fil. epithet cannot now be taken up in *Aptosimum.*

Regarding the varietal epithet *elongatum,* there is no evidence that Hiern based his var. *elongatum* on *A. elongatum* Engl. At varietal rank, therefore, Hiern's epithet has priority and must be transferred to *A. procumbens.* If, however, the entity should be reinstated as a separate species, the correct citation will be *A. elongatum* Engl.

L. E. CODD

THYMELAEACEAE

NOTES ON *GNIDIA*

In the Genera of Southern African Flowering Plants the genus *Gnidia* is interpreted by Dyer (1975: 393) in a wide sense to include the genera *Lasiosiphon, Arthrosolen, Pseudognidia, Basutica* and *Struthiolopsis* — an opinion I fully endorse, but with the addition of the genus *Craspedostoma* Domke as a further synonym. When treating *Gnidia* in this sense, some new names become necessary. Three are published in this note.

Gnidia albosericea *M. Moss* ex *Peterson,* nom. nov.

Lasiosiphon ornatus Burtt Davy, Fl. Transv. 1: 45, 206 (1926); Compton, Annot. Check List Flora Swaziland, Jl S. Afr. Bot., Suppl. 6: 56, 141 (1966) and Fl. Swazild, Jl S. Afr. Bot., Suppl. 11: 388 (1976), non *Arthrosolen ornatus* Meisn. in DC., Prodr. 14: 559 (1857), nec *Gnidia ornata* (Meisn.) Gilg in Engler & Prantl, Natürl. PflFam. 3, 6a: 228 (1894). Type: Swaziland, Hlatikulu, Dec. 1910, *M. M. Stewart* 14 (K, holo.!).

Because of the existence of the combination *Gnidia ornata* (Meisn.) Gilg for a conspicuous species found only in a few localities in the districts of Caledon and Bredasdorp, a new specific epithet must be given when transferring *Lasiosiphon ornatus* to *Gnidia. G. albosericea* is an unpublished name used by Mrs M. Moss on several herbarium labels for this species and I find it appropriate to use the specific epithet of this binomial.

The description of the species is maintained as in the original publication of *L. ornatus* by Burtt Davy.

G. albosericea is a grassland species in the eastern Transvaal, the highveld of Swaziland and northern Natal. It is very closely related to *G. splendens* Meisn. and a careful examination of the two species will very likely prove that they are conspecific.

Gnidia canoargentea (*C.H.Wr.*) *Gilg* in Engl., Pflanzenw. Afr. 3, 2: 634 (1921).

Lasiosiphon canoargenteus C. H. Wr. in T.-Dyer, Fl. Cap. 5, 2: 70 (1915), anglice, et in Kew Bull. 1916: 139 (1916), *'canoargentea'.* Type: Transvaal, Lydenburg District, in clivis montosis Lydenburg, June 1874, *McLea* in Herb. Bolus 3020 (K, lecto., selected by Burtt Davy). Paratype: Transvaal, Witte Kranz, near Lydenburg, Aug. 1885, *Wilms* 1298.

Lasiosiphon mossii Burtt Davy, Fl. Transv. 1: 45, 205, 206 (1926). Type: Transvaal, Witwatersrand District, Turffontein, Orange Grove, stony hills, 6. 7. 1919, *E. G. Bryant* G2 (K, holo.).

E. Gilg seems to have been the first to distinguish this species. He wrote the name *canoargentea* on the herbarium label of a specimen of *Wilms* 1298, apparently in the Berlin Herbarium. On the Kew sheet of *McLea in Herb. Bolus* 3020, N. E. Brown made the following note: '*Gnidia canoargentea* Gilg! Matches the type! (*Wilms* 1298, Witte Kranz near Lydenburg, Transvaal, Aug. 1885). Compared June 17, 1903'. However, the name was not published by Gilg until 1921, by which time the epithet had been used by C. H. Wright in *Lasiosiphon canoargenteus.*

Lasiosiphon mossii cannot be distinguished from *Gnidia canoargenteus.* This was observed by Mrs Moss in 1932, who labelled the type specimen of *Lasiosiphon mossii* as *Gnidia canoargentea.* Habit and general appearance are the same in the two species. In his key to *Lasiosiphon* Burtt Davy (1926) distinguishes *L. mossii* from *L. canoargentea* on (among other characters) the linear versus oblong petals, but this character does not hold. In *G. canoargentea* the apex of the petals varies from obtuse to emarginate (sometimes nearly bifid) even in the same flower.

G. canoargentea is very close to *G. splendens* Meisn. It is found only in the Transvaal, whereas *G.*

splendens has its main distribution in Natal with a few localities in the Transvaal, Swaziland and Lesotho.

Gnidia propinqua (*Hilliard*) *Peterson*, comb. nov.

Basutica propinqua Hilliard in Notes R. bot. Gdn Edinb. 31: 31 (1971). Type: Lesotho, 1 mile NNW of entrance to Bushman's River Pass, 5. 12. 1967, *Wright* 333 (NU, holo.; E, iso.!).

In addition to the specimens cited in the protologue, a few other collections can be mentioned:

NATAL.—Underberg District, near top of Mashai Pass, c. 2740 m, 7.11.1977, *Hilliard & Burtt* 10478 (E). Estcourt District, summit of Drakensberg, in vicinity of Giants Castle Pass, 3170 m, 19.11.1970, *Wright* 1031 (PRE).

LESOTHO.—Mokhotlong District, Sani Top, c. 2860 m, 31.12.1973, *Hilliard* 5408 (E, PRE); Sani Pass Summit, c. 1–2 km N of chalet, c. 2860 m, 13.1.1977, *Killick* 4095 (PRE).

Gnidia robusta *Peterson*, nom. nov.

Lasiosiphon nanus Burtt Davy, Fl. Transv. 1: 45, 207 (1926) non *Gnidia nana* (L. f.) Wikstr. in K. svenska Vetensk.-Akad. Handl. 1818: 316 (1818) (endemic in the south-western part of the Cape Province) nec *G. nana* Eckl. & Zeyh, ex Meisn. in DC., Prodr. 14: 583 (1857), quae = *G. sericea* L. Type: Swaziland, Hlatikulu, s. dat., *M. M. Stewart* s.n. (K, holo.!).

L. robustus M. Moss ex Compton, nom. non rite publ., Annot. Check List Flora Swaziland, Jl S. Afr. Bot., Suppl. 6: 58 (1966) and Flora Swaziland, Jl S. Afr. Bot., Suppl. 11: 388 (1976).

This species resembles the very variable *Gnidia caffra* (Meisn.) Gilg, but differs in being more robustly branched, more densely leaved and having conspicuous petals, 4–6 mm long × 2–3 mm broad (in *G. caffra* minute, up to 1 mm long).

When comparing the type of *Lasiosiphon nanus* with specimens of *Lasiosiphon robustus* named by Mrs Moss and R. H. Compton it is evident that these species are conspecific. The structure of the flowers in the two species is identical. The type of *L. nanus* consists of only four small branches. This evidently influenced Burtt Davy to choose the specific epithet '*nanus*', an epithet which cannot be used when transferring *L. nanus* to the genus *Gnidia* because of the prior existence of *G. nana* (L. f.) Wikstr.

Lasiosiphon robustus was distinguished and tentatively named by Mrs M. Moss, who worked on the Transvaal Thymelaeaceae for a long time. However, she never published this name, which was later taken up, but not validated by R. H. Compton in his Flora of Swaziland. For some reason Compton failed to mention *L. nanus* either in his Check List or in the Flora of Swaziland.

Gnidia robusta is reported from the eastern Transvaal, Swaziland and Natal (Paulpietersburg, Vryheid and Ngotshe Districts).

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Speciation environments and centres of diversity in southern Africa. I. Conceptual framework

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ABSTRACT

A knowledge of the nature and distribution of the environments where speciation (micro-evolution) is or has been rapid would help explain plant distributions and give insight into the mechanisms of plant evolution. Before southern African speciation environments can be identified and described, a number of basic theoretical concepts have to be clarified. In this paper the major taxonomic, systematic, floristic, ecological and evolutionary ideas pertinent to speciation environments are reviewed and discussed. Despite many publications about species concepts, species diversity, modes of speciation and the relationship between environments and genetic variability within taxa, it is still not possible to make predictions about the kinds of environments that favour speciation.

INTRODUCTION

A speciation environment is considered to be a place where speciation (micro-evolution) is particularly rapid, or has been so in the recent past. It would be informative to determine speciation environments for taxa and for regions, both to clarify species distribution patterns and to give insight into the mechanisms of micro-evolution. When seeking environments where taxa show evidence of proliferation and to correlate this proliferation with measurable environmental variables, it is necessary to link the disciplines of ecology, evolutionary biology, systematics and taxonomy. Such interdisciplinary work can be hazardous because the weaknesses of hypotheses and the assumptions on which they are based are often not explicit. In the sections which follow some of these troublesome concepts are discussed in order to show the contribution of each to our understanding of speciation environments.

TAXONOMY, SYSTEMATICS AND FLORISTICS

Chorologists, phytogeographers and community ecologists base much of their work on the names of taxa, but so far stability of names has not yet been attained, either because of differences in taxonomic treatment ('lumping' or 'splitting' of taxa) or because of changes made necessary by the rules of nomenclature. This is such a familiar problem that it will not be considered any further; it is enough to say that name changes alter one of the main elements used by other disciplines.

Related to the problem of name changes is the problem of species concepts. This has been the subject of many publications, such as the papers in Slobodichikoff (1976), but as Paterson (1981) has pointed out, there is still little agreement on what constitutes a species. Biological species are groups of individuals which exchange genetic material within the species but not with other species. They may be defined by reproductive isolation in the sense of Dobzhansky (1970) or Mayr (1970), or by the existence of specific mate recognition systems (Paterson, 1980). Taxonomic species are recognized on the basis of many features, but maintenance of genetic integrity is incidental and not central. The taxonomic species is the species concept of virtually all floras for the majority of species (Davis & Heywood, 1963, p. 94). In studies of speciation the plant groupings considered must have the potential to evolve, so the biological species and not the taxonomic species concept must be employed. Inferences about the species richness or degree of evolutionary activity in an area can only be based on enumeration of biological species. However, it is usually not possible to determine what proportion of a Flora is composed of non-biological species.

Species diversity is often used in phytogeography, ecology and evolutionary biology. Several aspects of diversity are distinguished:

1. Habitat diversity, which is subdivided into within-habitat (alpha) diversity and between-habitat (beta) diversity (MacArthur, 1965; Whittaker, 1972);

2. Species diversity, also called gamma diversity (Whittaker, 1972). Alpha and beta diversity are the measures most used by ecologists, while taxonomists, phytogeographers and evolutionists use gamma diversity as the measure of species richness in an area. Richerson & Lum (1980) point out that evenness of distribution in numbers of individuals among species is just as important a component of diversity as species richness because it is a measure of how evenly resources are partitioned among taxa and hence is an indicator of the degree of interaction between components of an ecosystem.

Species diversity has bearing on photogeography because high diversity for an area will be the result of one or all of the following: rapid speciation with correspondingly low extinction rates; high immigration rates; large pools, or several different pools, from which elements of a flora have been drawn; and the type of environment which encourages diversity. As Gentry (1981) points out, a high concentration of species in an area can be due to gamma, alpha or beta diversity, or to combinations of these. If concentration is a result of high gamma diversity then local endemism is likely to be important; if due to high alpha diversity, it means that the plant communities are richer in numbers of species than the same communities elsewhere; and if due to beta diversity, then many different communities, each having a distinctive species complement, are 'packed' into the area. It is therefore important that the type of diversity is specified when discussing environments, selection pressures, species interactions, etc. Areas of maximum diversity, either alpha, beta or gamma, are not necessarily evolutionary cradles. Speciation is only one of a number of mechanisms leading to high levels of diversity, and some kinds of speciation may reduce alpha or gamma diversity.

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Furthermore, despite the large theoretical and applied literature on the subject, the mechanisms underlying differences in diversity are still imperfectly known. Richerson & Lum (1980) show that it is not yet possible to predict even whether environmental stability or instability is most likely to be correlated with maximum gamma diversity for an area.

ECOLOGY

In finding an environment in which speciation has been rapid we hope to find the mechanisms (selective pressures) that have encouraged micro-evolution in taxa or habitats. Many of these selective pressures are ecological, and may be grouped into abiotic environmental differences; biotic interactions such as competition, predation/parasitism, symbiosis and mimicry; or factors related to levels of complexity of the biocoenosis such as stability and resilience. In some cases the assumptions underlying these ecological concepts are imprecise or only partly tested, yet the concepts are taken as proven by workers in other fields.

1. *Abiotic environmental differences*

Different abiotic environments will exert different selection pressures on organisms, but general principles describing the direction and magnitude of selection of different environments have not been formulated. For example, it is not possible to predict the effect of environmental stability on gamma diversity (Richerson & Lum, 1980) or intraspecific genetic heterogeneity (Hamrick *et al.*, 1976).

2. *Biotic interactions: competition*

Competition is the biotic interaction most often considered as a selective force (*e.g.*, 'survival of the fittest'). There is a large amount of literature on the effects of intra- and interspecific competition. Gause (1934), Beals (1968), Bartholomew (1970), Levin & Anderson (1970), Horn & MacArthur (1972), Miles (1974), Schaffer (1977), Waser (1978) and Berendse (1979, 1981) give a representative sample of the range of situations and effects of competitive interactions. Evolutionarily, and in some cases even ecologically, competition is not as clearly effective as the competitive exclusion principle (Hardin, 1960) or the phenomenon of character displacement (Brown & Wilson, 1956) suggest. In fact, certain authors seriously question both the role of competition in determining the coexistence or extinction of populations (*e.g.*, Elton (1958) for the replacement of red squirrels by grey squirrels in Britain), and the role of reinforcement in speciation (see Paterson (1978) for examples). Competitive interactions can be quite complex. Leeuck & Rice (1976) showed that *Aristida oligantha* is able to dominate old field seral stages for extended periods because of the negative effects of its rhizophore bacteria upon nitrogen fixing bacteria associated with species of later seral stages. In this case a superficially simple case of competition is really the result of a number of kinds of interactions. The effects of competition, and of other kinds of interactions, must be critically appraised for each situation. As Janzen's data (Janzen 1969, 1971) and hypotheses (*e.g.*, Janzen 1976, 1977) show, it is far easier to pose questions about the effects of interactions than to illustrate their action as selective forces.

3. *Stability and resilience of communities*

The ecosystem concepts of stability and resilience are sometimes misapplied, and since stability is often considered to be central to diversity, there is a need for clarification. Stability is the property allowing an ecosystem to resist small disturbances and promoting the recovery of the system if disturbances occur. (Holling, 1973). As Walker (1980) and Walker *et al.* (1981) have pointed out, stable systems have low variability, and if they do change much they will not return to their former equilibrium states. Stable systems provide environments that show little change through time. By contrast, resilient systems may be changed considerably by disturbances yet still return to their equilibrium states (Holling, 1973; Walker, 1980). Resilient systems show high variability, are often unstable, and hence provide temporally heterogenous environments. Our knowledge of the relationships between stability, resilience and species diversity is still imperfect, and their importance to speciation cannot be predicted.

Closely related to stability, resilience and spatial heterogeneity is the question of intraspecific genetic variability. Reviews such as those by Hamrick *et al.* (1976) and Hedrick *et al.* (1979) and research papers such as those of Antonovics (1968), Tigerstadt (1973), Babbel & Selander (1974) and Bosbach & Hurka (1981) show that there is still much to learn. For example, marginal populations are frequently phenotypically less variable than those from the centre of a species range (Soule, 1973), but a number of contradictions to this conclusion have been reported [*e.g.*, Tigerstadt (1973) and Bosbach & Hurka (1981)]. These conflicting data suggest that the underlying principles are still not understood.

EVOLUTIONARY THEORY

There are numerous hypotheses for the mechanisms leading to speciation but, as Paterson (1981) points out, only a few are supported by data. There is also little information about the evolutionary behaviour of a taxon in response to different ecological situations, or about the selective effects of the same ecological conditions on different taxa. Genetic variability within a species or population is the basis for micro-evolution under differential selection pressure, and it would be helpful to be able to predict localities where genetic variability is likely to be high. Unfortunately, as increasing numbers of taxa are studied, it is clear that the kinds of genotypes that 'fit' particular environments cannot be postulated (Bosbach & Hurka, 1981).

Stebbins's (1974) concept of canalization of genotypes as a result of their evolutionary history has received too little attention. Both Stebbins (1974) and Riedl (1977) indicate the possible importance of the degree of canalization of the genotype and the existence, degree and nature of within-genotype hierarchies on subsequent genetic ability, but these hypotheses have not yet been tested by experiments.

Modes and concepts of speciation

Speciation is a primary process leading to patterns of plant distribution and is central to taxonomy and evolutionary study. Underlying its significance, Clayton & Cope (1980) list the introduction of species and the origin of new species as one of the major sources of discrepancy between boundaries of phytochoria and phytogeographical formations.

Evolutionary biologists, taxonomists, phytogeographers and chorologists are interested in the process and outcome of the splitting of populations into taxa or reproductively separate lineages. This phenomenon is called cladogenesis by Dobzhansky (1937), true speciation by Mayr (1963) and primary speciation by Grant (1971). It is contrasted with the process in which a species changes through time but does not split, which Dobzhansky (1937) called anagenesis and Mayr (1963) called phyletic speciation. Phyletic speciation may be the result of mutations (autogenous) or introgression (allogenous), the latter being equivalent to Grant's (1971) secondary speciation.

Whenever true speciation is discussed, only the biological concept of species can be considered. This means that only sexually reproducing organisms can be accepted as species. Zoologists are therefore seldom faced with situations where agamospermy is facultative, which is the case for a considerable number of plant species (see for example Gustafsson 1946 & 1947; Brown & Emery, 1958; Asker, 1979), or where cleistogamy and chasmogamy occur together (*e.g.*, Maheshwari & Baldev, 1958; Schemske, 1978). This means that while the agomospheric plants are reproducing asexually they cannot be considered as part of a species population. However, under these conditions, the argument that new genotypes will be 'swamped by pollen from more numerous individuals', made so strongly by Levin (1975) and Paterson (1981), probably does not hold. As Tothill (1966) has indicated for *Heteropogon contortus,* frequent agamospermic reproduction together with sexual reproduction is a powerful mechanism allowing differentiation of gene pools even in the face of strong pollen flow. All of the above means that botanists must be wary of accepting evolutionary models that do not recognize that the flexibility of the reproductive biology of many advanced plants is far greater than that found in most animals.

The literature on cladogenesis is extensive and only some of the proposed models will be discussed here, to show the difficulties that arise in trying to use these models for interpretation. More complete treatments of cladogenesis are to be found in Grant (1971), Mayr (1963) and White (1968). The commonest form of speciation apparently occurs when populations become spatially isolated and then differentiate as a result of genetic rearrangements. If the differentiation is sufficiently great that the segregates are reproductively isolated if (or when) they become sympatric once more, then speciation has taken place. This is the classic 'species pump' hypothesis of Valentine (1967), and is the only mode of speciation which Paterson (1981) recognized as being supported by observed critical facts. The process is called allopatric speciation and its importance has been shown by many studies.

Sympatric speciation, where fragmentation of a gene pool occurs without spatial separation, was shown to be theoretically possible as long as there are different niches available and the selective advantages are high for different genomes in different niches (Maynard Smith, 1966). Bush (1969, 1974) has advocated sympatric speciation as the mode whereby sibling of fruit flies have evolved, but Paterson (1981) argues that the case presented by Bush is inconclusive. Paterson's own argument against sympatric speciation by the formation of alloploids is, however, also invalid because of his assumptions about plant reproductive strategies. Sympatric speciation is therefore seen as a mode supported by little evidence, which might be more applicable to plants than to animals.

Two refinements of the concept of sympatric speciation are parapatric and stasipatric speciation. In parapatry, differentiation occurs between populations in the same geographical region, but in different habitats or niches. Lewis & Raven (1958) reported sympatric speciation in diploid species of *Clarkia* in response to edaphic factors, and Gentry (1981) has reported micro-evolution in response to edaphic factors in *Passiflora.* It is possible that high beta diversity is an indicator that parapatric speciation has taken place, but data are few at this stage and no conclusion can be drawn. In stasipatry, White (1968) states that chromosomal rearrangements occur within the range of the species, and as a result of the superior performance of the new genome, spread through the range of the parental species. Lewis (1966) pointed out that rapid chromosome reorganization in marginal populations is a frequent mode of plant speciation, and as we discuss elsewhere (Gibbs Russell & Robinson, in press), we believe that stasipatric and perhaps parapatric speciation is of considerable importance to the development of the African flora.

Paterson (1981) warns of the difficulties of most of the models of speciation but, as Jameson (1977) has stressed, it is unlikely that a single model will hold for all situations. Since the mode (or modes) of speciation will determine where differentiation will be rapid and the kind of taxa that are likely to be evolving rapidly, it is too early to assume that there is only one model of speciation, particularly for plant taxa which show great flexibility in their reproductive biology.

The kind of speciation referred to by Grant, Dobzhansky, Mayr and others deal primarily with changes through time, but do not consider the phytochoria where they occur. Data from the eastern Cape (Gibbs Russell & Robinson, 1981) suggest that the type of speciation may be linked to the phytochorion and hence that it may be necessary to take account of where speciation occurs relative to the area of major adaptive radiation of a taxon. As a result we feel it is necessary to introduce terms linking the process of speciation to the phytochorion where it is taking place.

a. phytochorial sympatry: speciation in the phytochorion where major adaptive radiation of the group occurred.

b. phytochorial allopatry: speciation in a phytochorion other than the one where major adaptive radiation of the group occurred.

A mode of speciation which has received too little attention is that of allogenous phyletic speciation. Here, new species are formed as a result of introgression from other taxa. In some cases this may lead to a reduction in species numbers if species boundaries are sufficiently blurred, and may result from migration of a derived species back into the range of a parental or sibling species. In southern Africa, where much of the flora is derived from tropical taxa, it is possible to envisage evolution taking place in a series of steps. Allopatric, parapatric or stasipatric could lead to the evolution of derived species in phytochorial allopatry, or to narrowly endemic species in phytochorial sympatry. Allogenous phyletic speciation may then occur as derived genetic segregates, which have become differentiated to some extent, exchange genes with parental, sibling or other species.

Proposed speciation environments

The environment in which speciation takes place is as important as the mode of speciation. Such areas will not necessarily have high alpha, beta or gamma diversity. Phyletic speciation, while changing the nature of taxa of an area through time, does not result in an increase in the numbers of species, and allogenous phyletic speciation may even reduce gamma diversity. By contrast, Gibbs Russell & Robinson (1981) show that high gamma diversity can result simply from close juxtaposition of a number of phytochorial elements with apparently low speciation rates. If speciation environments could be recognized, either in general or for specific taxa, our understanding of the mechanisms of micro-evolution would be advanced and predictions about man's impact on the flora of the future may possibly be made. A number of types of environments have been suggested as particularly conducive to micro-evolution.

(a) *Tropical environments*

The high gamma diversity found in many tropical regions has long been taken to indicate that this was the type of environment where speciation was most rapid. Countering this, Stebbins (1974) suggested that tropical areas, specifically the forests, are museums. Both viewpoints are probably too narrow, and at least some plant groups are evolving rapidly in tropical forest environments. Evolution here is often in response to biotic factors (*e.g.*, pollinators in the orchids). Simpson (1977) pointed out that there is no reason to suppose that tropical forests provide less opportunity for species proliferation than do other environments. From the general point of view, the significance of tropical environments is that climatic conditions are stable and favourable for a wide range of plants.

(b) *Fluctuating environments, often ecotones*

Environmental fluctuations can isolate populations and thereby accelerate allopatric speciation by the 'species pump' mode of Valentine (1967). Peripheral populations may become isolated, or populations may be established beyond the optimum range during exceptionally favourable periods. When conditions become severe these populations may be isolated and differentiate. Both Stebbins (1972, 1974) and Valentine (1967) take instability as the key environmental feature encouraging species formation.

(c) *Arid regions*

The hypothesis that arid regions are centres of speciation, strongly advocated by Stebbins (1952), Raven (1964) and Axelrod (1972) is really a variant of fluctuating environments as a stimulus to speciation since arid areas are usually characterized by fluctuations of climate.

(d) *Fine-scale spatial heterogeneity*

Topographic, edaphic or other environmental heterogeneity is generally assumed to encourage fragmentation by providing isolated microhabitats close together. The work of Lewis & Raven (1958) on *Clarkia* and of Gentry (1981) on *Passiflora* are examples of this. From these studies it seems that edaphic heterogeneity alone may promote speciation in stable environments.

The variety of environments that have been suggested as favourable for speciation shows that it is still not possible to state unequivocably that a single kind of environment promotes gene pool fragmentation. Spatial heterogeneity, instability and the complexity of biotic interactions all seem significant for some groups or in some areas. The difficulty of making predictions about speciation environments is increased because there are no clear-cut relationships between stable or resilient ecosystems, particular environments and rates of speciation.

CONCLUSION

Many of the concepts that have a bearing on speciation and speciation environments have their own internal uncertainties. It is therefore difficult to combine them to make interpretations, establish tests of hypotheses or derive general principles. Nevertheless, we believe that attempting to define speciation environments provides a useful change of perspective in studying the mechanisms of evolution of the southern African flora, and hence of explaining patterns of distribution of taxa.

ACKNOWLEDGEMENTS

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UITTREKSEL

Kennis van die aard en verspreiding van omgewings waar spesiasie (mikro-ewolusie) vinnig plaasvind of plaasgevind het kan nuttig wees om die verspreiding van plante te verduidelik en kan insig gee in die meganismes van plantewolusie. Voordat die Suider-Afrikaanse spesiasie omgewings geïdentifiseer en beskryf kan word, moet 'n aantal basiese begrippe opgeklaar word. In hierdie artikel word die vernaamste taksonomiese, ekologiese en ewolusionêre begrippe wat betrekking het op die spesiale omgewings hersien en bespreek. Daar word aangetoon dat ten spyte van baie publikasies oor spesies begrippe, spesiesdiversiteit, maniere van spesiasie en die verwantskap tussen die omgewing en intra-takson genetiese variasie, nie een van die begrippe verfynd is tot op die punt waar voorspellings gemaak kan word nie.

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Bothalia 14, 1: 89–93 (1982)

Leaf anatomy of the South African Danthonieae (Poaceae). VI. *Merxmuellera arundinacea* and *M. cincta*

R. P. ELLIS*

ABSTRACT

The leaf blade anatomy and the abaxial epidermal histology of *Merxmuellera arundinacea* (Berg.) Conert and *M. cincta* (Nees) Conert are described and illustrated. These two species resemble one another morphologically and are the only representatives of the genus with open, expanded leaves. They are, nevertheless, clearly distinct anatomically, particularly in the structure of the leaf blade as viewed in transverse section. The anatomy of *M. cincta* is noteworthy in the possession of additional vascular bundles located immediately below the first order vascular bundles. This vertical arrangement of bundles at differing levels is a unique feature of *M. cincta* and possibly indicates a need for taxonomic adjustment.

INTRODUCTION

Merxmuellera arundinacea (Berg.) Conert [= *Danthonia arundinacea* (Berg.) Schweick.] and *M. cincta* (Nees) Conert (= *D. cincta* Nees) (Conert, 1970) are both robust, reed-like, tufted perennials forming large, dense tussocks, 0,5–1 m in diameter. Their leaf blades are long and lax being from 60–100 cm long. The growth form of these two species is therefore very similar and superficially they resemble one another very closely, especially in the vegetative condition. Anatomically these species both have open, expanded leaf blades — a condition not found in any of the other *Merxmuellera* species occurring in South Africa.

In contrast to these similarities, several morphological, anatomical and ecological differences satisfactorily separate these two species. Thus the fringe of hairs across the lemma, the longer glumes, the inconspicuous central awn and the longer ligule distinguish *M. cincta* from the smaller *M. arundinacea* (Chippindall, 1955). The stout culms of *M. arundinacea* are only up to 1 m high whereas in *M. cincta* they can reach 2 m. The present study also shows that these species are separated ecologically and that they bear very little anatomical resemblance to one another apart from having wide expanded leaf blades. This anatomical evidence does not indicate a close relationship between *M. arundinacea* and *M. cincta* and actually appears to suggest that *M. cincta* may be incorrectly placed in the genus *Merxmuellera* and possibly even in the Danthonieae.

The terminology used in the ensuing anatomical descriptions is according to Ellis (1976, 1979) and the following abbreviations will be used:

vb/s—vascular bundle/s
1'vb/s—first order vascular bundle/s
2'vb/s—second order vascular bundle/s
ibs—inner bundle sheath; mestome sheath
obs—outer bundle sheath; parenchyma sheath

ANATOMICAL DESCRIPTION OF *MERXMUELLERA ARUNDINACEA*

Leaf in transverse section

Leaf outline: flat, expanded; often broadly U-shaped; greater than 5 mm wide and between 0,36 mm and 0,45 mm thick. *Ribs and furrows:* deep, cleft-like adaxial furrows between all vbs; inversely Y-shaped. Massive, flat-topped (Figs 2 & 3) or rounded (Fig. 1) adaxial ribs associated with 1'vbs; smaller rounded or triangular ribs overly 3'vbs. Abaxial surface without ribs and furrows. *Median vascular bundle:* not structurally distinct from lateral 1'vbs. *Vascular bundle arrangement:* one 3'vb between consecutive 1'vbs; no 2'vbs; 15 or more 1'vbs in section. All vbs located slightly to the adaxial side of the blade (Figs 1–3). *Vascular bundle structure:* vbs elliptical; metaxylem vessels narrow with circular lumens. No additional bundles developed in massive ribs associated with 1'vbs as in *M. cincta* (Figs 7–9). *Vascular bundle sheaths:* double; obs elliptical or horse-shoe-shaped; wide interruptions both adaxially and abaxially; no extensions; obs cells small; elliptical and not larger than mesophyll cells; chloroplasts lacking. Ibs complete with secondary walls very thick. *Sclerenchyma:* adaxial girders well developed; inversely anchor-shaped with long, sturdy stem in association with 3'vbs but T-shaped with short, sturdy stem and long horizontal cross-piece in association with 1'vbs. Continuous abaxial hypodermal band extending as trapezoidal or tall, stout vertical columns to the 1'vbs and 3'vbs; these girders interrupt the obs; consist of very thick-walled fibres. Leaf margin with small sclerenchyma cap (Figs 1 & 3). *Mesophyll:* not radiate; composed of small, isodiametric cells; tightly packed with insignificant air-space system even adjacent to the stomata; mesophyll tissue in W-shaped groups occupying sides and bases of furrows. *Colourless cells:* absent. *Adaxial epidermal cells:* small fan-shaped groups of bulliform cells located at the bases of furrows; cells small, not larger than obs cells. No macro-hairs, hooks, prickles or cuticular papillae. Outer tangential cell walls somewhat arched. *Abaxial epidermal cells:* no bulliform cells, stomata, macro-hairs, hooks or papillae. Angular prickles developed near margin (Fig. 1). Continuous, thick cuticular layer covers outer tangential wall of all cells.

Abaxial epidermis

Intercostal zones: not differentiated. *Stomata:* none present. *Papillae:* absent. *Hairs:* micro-hairs, macro-hairs, hooks and prickles not present on this surface except along margin where angular prickles

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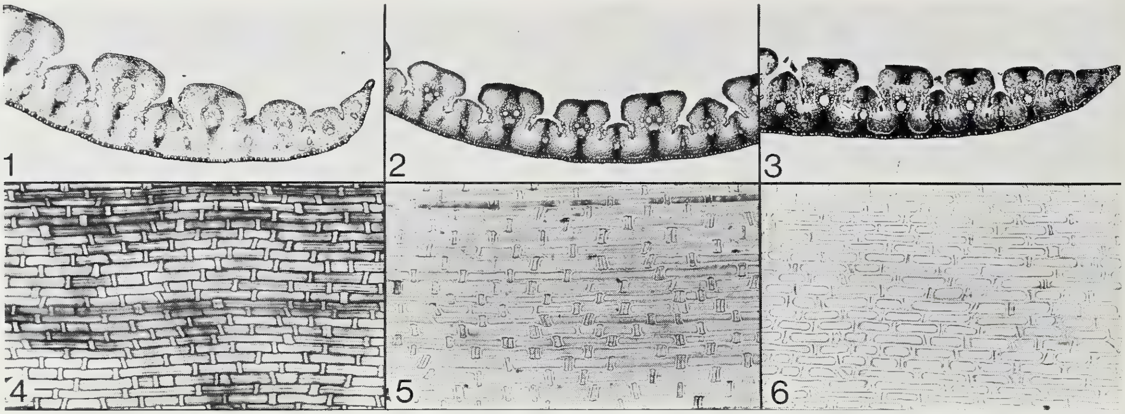


FIGS 1–6.—Leaf blade anatomy of *Merxmuellera arundinacea*. 1–3, leaf blade in transverse section. All × 100. (1, *Ellis* 2503; 2, *Ellis* 1707; 3, *Ellis* 2474.) 4–6, abaxial epidermis as seen in surface view. All × 400. Note absence of intercostal zones. (4, *Ellis* 1707; 5, *Ellis* 1149; 6, *Van Breda & Joubert* 1999.)

are found; large bases with barbs of medium length. *Silica bodies:* tall and narrow, vertically elongated rectangular; smooth; regular outlines; same width or sometimes slightly wider than costal long cells in same file; present equally throughout abaxial epidermis; usually solitary but sometimes paired (Figs 4–6). Silica often not developed in silica cells. *Costal cell arrangement:* single, seldom paired, costal short cells alternate with single costal long cells throughout the abaxial epidermis; long cells elongated, with straight walls (Fig. 4), pitted (Figs 5 & 6) and often filled with air (Fig. 6). Arrangement of adjacent horizontal files alternates.

Specimens examined:

CAPE.—3119 (Calvinia): Kobe Mts, Vanrhynsdorp (–CA), *Ellis 2448.* 3219 (Wuppertal): Pakhuis Pass, Clanwilliam (–AA), *Ellis 709, 1149, 1707;* Blinkberg Pass, Skurweberge (–CD), *Ellis 2503.* 3318 (Cape Town): Honigberg, Piketberg (–BB), *Acocks 23433.* 3319 (Worcester): Gouda, near Tulbagh (–AC), *Esterhuysen 18828;* Swartruggensberge (–BA), *Ellis 2474;* Robertson (–DD), *Von Breda & Joubert 1999.*

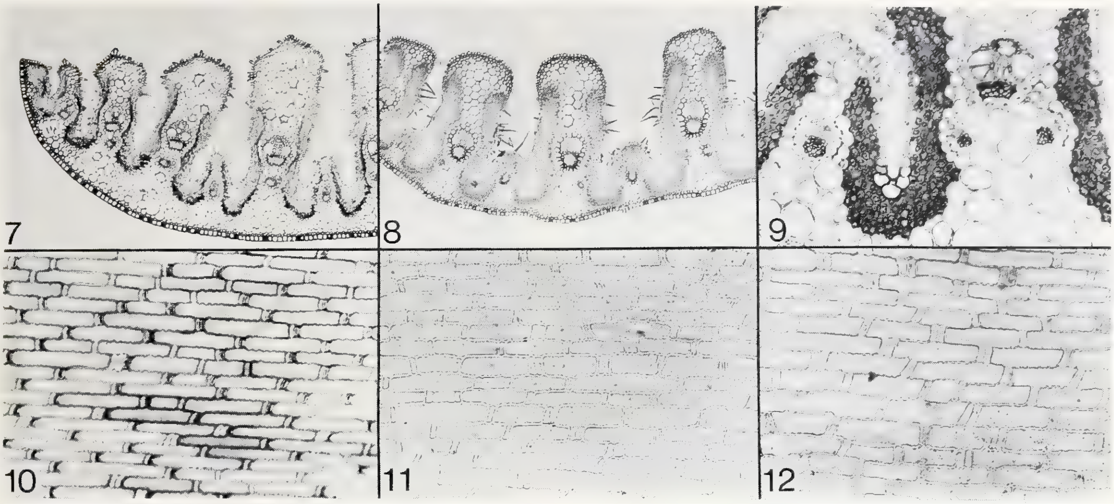
ANATOMICAL DESCRIPTION OF *MERXMUELLERA CINCTA*

Leaf in transverse section

Leaf outline: U-shaped; either open, almost fully expanded to tightly infolded and elliptical. Leaves wide (1,5 mm–3,5 mm) and exceptionally thick (> 0,5 mm). *Ribs and furrows:* tall, massive adaxial ribs associated with 1'vbs; more than 3× taller than ribs over 3'vbs; bases narrow and broad apices either angled (Fig. 7) or rounded (Fig. 8). Furrows deep, more than half the leaf thickness but width varies depending on degree of infolding of leaf; Y-shaped in tightly infolded leaves. No abaxial ribs or furrows. *Median vascular bundle:* distinguishable by location only. *Vascular bundle arrangement:* one 3'vb between successive 1'vbs; no 2'vbs; 9–13 1'vbs in blade; bundles located centrally in blade. *Vascular bundle structure:* unique additional small bundles associated with all 1'vbs in all specimens except *Comins* 974 where they are absent; these bundles consist of second, third and even fourth groups of vascular tissue located immediately below the 1'vbs near the bases of the massive ribs at a lower plane (Fig. 9); phloem tissue of these bundles well developed and they are surrounded by a distinct, thickened sheath (Fig. 9). 3'vbs relatively large and circular or elliptical in shape; 1'vbs egg-shaped; metaxylem vessels relatively wide; no sclerosis of the phloem. *Vascular bundle sheaths:* double; obs tall and complete; cells round, inflated and without chloroplasts; broad, well-developed adaxial and abaxial extensions of large, thin-walled colourless cells present in association with 1' and 3'vbs; adaxial extensions somewhat inversely anchor-shaped and abaxial extension may extend into continuous abaxial hypodermal parenchyma layer (Fig. 7). Ibs entire; walls uniformly thickened; cells about same size as adjacent obs cells. *Sclerenchyma:* adaxial strands in 1'vb ribs subepidermal and arched to follow shape of rib; abaxial sclerenchyma thin, continuous hypodermal layer not associated with vbs. Cells relatively large in T.S., lignified, but with little secondary wall development (Fig. 9). *Mesophyll:* not radiate; small isodiametric cells, tightly packed but tending to become circular with development of an air-space system (Fig. 9); confined to W-shaped groups on sides and bases of furrows. Lacunae appear to be present in the mesophyll at the bases of furrows in some of the herbarium specimens from which sections were made. *Colourless cells:* abaxial side of leaf almost entirely comprised of regular, colourless collenchyma (Fig. 7). *Adaxial epidermis:* fan-shaped groups of small bulliform cells present at bases of furrows; elongated prickle hairs common on sides of furrows (Fig. 9); no papillae; costal zones at apices of massive ribs, intercostal zones along sides. *Abaxial epidermis:* distinct, thick cuticle continuous over abaxial epidermal cells; no bulliform cells, papillae, prickle-hairs or stomata; not divided into costal and intercostal zones.

Abaxial epidermis

Intercostal zones: not differentiated. *Stomata:* not present on abaxial surface. *Papillae:* absent. *Hairs:* prickles, micro-hairs and macro-hairs not present on



FIGS 7–12.—Leaf blade anatomy of *Merxmuellera cincta*. 7–9, leaf blade in transverse section. (7, *Acocks* 20044, × 100; 8, *Ellis* 2332, × 100; 9, *Ellis* 3268, × 400. Note presence of small vascular bundles beneath first order bundle.) 10–12, abaxial epidermis. All × 400. Note absence of intercostal zones. (10, *Ellis* 3268; 11, *Ellis* 2331; 12, *Ellis* 2332.)

this surface. *Silica bodies:* vertically elongated; tall and narrow to elliptical in shape; outline smooth and regular; no granules; same width as adjacent long cells; similar silica bodies present throughout abaxial epidermis. *Costal cell arrangement:* paired or single costal short cells alternate with single costal long cells along all horizontal files; long cells only about 3× as long as wide; arrangement and structure similar throughout abaxial epidermis except that adjacent horizontal files arranged so that long cells and silica cell pairs are opposite one another in a brick-work pattern.

Specimens examined:

CAPE.—3228 (Butterworth): Kei Mouth (–CB), *Flanagan 2586*. 3318 (Cape Town): Jonkershoek, Stellenbosch (–DD), *Taylor 4511*. 3325 (Port Elizabeth): near Sea View (–DC), *Acocks 21447*. 3326 (Grahamstown): Grahamstown Nature Reserve (–BC), *Comins 974*. 3418 (Simonstown): Cape Hangklip (–BD), *Ellis 2331, 2332*. 3419 (Caledon): Riviersonderend (–BB), *Taylor 4492*. 3423 (Knysna): Tsitsikama, Storms River (–BB), *Ellis 3268*. 3424 (Humansdorp): Karreedouw (–BB), *Acocks 20044*.

DISCUSSION AND CONCLUSIONS

The anatomy of *M. arundinacea* is typical of the genus and it resembles the *M. disticha* (Nees) Conert group of species in leaf anatomy and epidermal histology (Ellis, 1981a). The alternating sequence of the first and third order vascular bundles along the width of the lamina is characteristic of this group of species which includes *M. disticha*, *M. davyi* (C. E. Hubb.) Conert and *M. macowanii* (Stapf) Conert. The adaxial ribs and furrows, the shape of the mesophyll groups and the structure of the silica bodies and costal long cells conform closely to the condition described for *M. macowanii* (Ellis, 1981a). The open, expanded nature of the leaf blade and the absence of adaxial prickles and papillae in *M. arundinacea* are the only anatomical differences noted between these two species. Even these differences are not absolute, however, and in some specimens of *M. arundinacea* a few prickle-like protuberances can be seen (Fig. 1) and the leaves of *M. macowanii* appear to be capable of opening to at least 45° (Ellis, 1981a). The relationships of *M. arundinacea* would, therefore, appear to be closest to *M. macowanii* and its relatives and leaf anatomy confirms its placement in this genus.

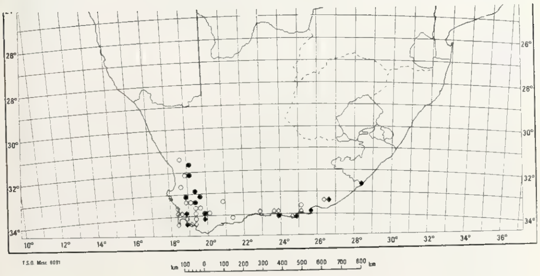


FIG. 13.—Distribution of *Merxmuellera arundinacea* (O) and *M. cincta* (◇) in the Cape Province of South Africa. Shaded symbols represent localities of specimens studied anatomically. Compiled from specimens in the National Herbarium, Pretoria (PRE).

Ecologically *M. arundinacea* is a species found on barren, quartzite mountain slopes of the Cape folded belt of the southern and south-western Cape Province (Fig. 13). It appears to be restricted to Table Mountain Sandstone and may become dominant on lower slopes, particularly those with a hot, northern aspect. It therefore has a more southerly distribution than *M. macowanii* which is only found as far south as the Stormberge of the north-eastern Cape but which also occurs on Table Mountain Sandstone in the midlands of Natal.

M. arundinacea obviously favours arid conditions but it is unusual in possessing wide expanded leaf blades and not acicular, permanently infolded leaves which are usually associated with grasses from dry environments. Closer examination of the anatomy of *M. arundinacea* does reveal that it actually possesses several adaptations that undoubtedly limit water loss. Thus the leaves have no abaxial stomata and the abaxial epidermis is underlaid by well-developed and heavily lignified sclerenchyma. The stomata are localized in a narrow band on the lower parts of the vertical sides of the cleft-like adaxial furrows. The upper parts of the massive ribs are sclerified and without stomata. Contact with the external atmosphere is consequently restricted to a very narrow aperture beneath the bulge of the ribs (Figs 1–3). *M. arundinacea* is notable in that these furrows retain their narrow, cleft-like form even in fully turgid, expanded leaves. In addition, the whole blade is capable of inrolling from both margins forming a hollow cylinder. This probably occurs under extremely adverse drought conditions and further limits evapotranspiration to a narrow opening between the closely opposed leaf margins.

M. cincta has a distributional range closely approximating that of *M. arundinacea* except that it occurs on the seaward side of the Cape mountain ranges (Fig. 13). In contrast to *M. arundinacea* it is a water-loving species found on streambanks, small vleis and in seepage areas. Sandy, poorly drained soil is preferred and it is sometimes found near the sea-shore to within about 50 m of the high water mark. These habitat differences between these two species are reflected in their leaf anatomy as described above.

The leaf anatomy of *M. cincta* is not typically that of a hydrophyte however, and the anatomical indications are that it may be a halophyte similar to *Ammophila arenaria* Link. of the Agrostideae — a species it resembles closely in anatomical and epidermal structure. It is, therefore, possible that *M. cincta* prefers moist conditions with high salinity or is adapted to survive regular dry conditions. *M. cincta* accordingly displays several desiccation reducing characteristics. The leaves can thus infold tightly forming a narrow adaxial channel, there are no abaxial stomata and it has a well-developed abaxial cuticle and waxy layer. When moisture conditions are favourable or excessive it would appear that transpiration can be enhanced by the leaf expanding with a consequent opening up of the adaxial furrows containing the stomato. There is also a well-developed vascular system with wide metaxylem vessels (Fig. 9) and a tendency for the development of an air-space system with diffuse mesophyll cell arrangement immediately adjacent to the stomatal apertures (Fig. 9). This condition has also been noted in the alpine bog forms of *M. disticha* (Ellis, 1980) and *M. stricta* (Schrad.) Conert (Ellis, 1980a), two other hygrophilous *Merxmeullera* species. In these respects *M. cincta* differs considerably from *M. arundinacea.*

Lacunae, which are typical of most hydrophytes, are not present in *M. cincta* specimens except in some plants collected from the eastern Cape at Port Elizabeth, Grahamstown and Kei Mouth (*Acocks* 21447, *Comins* 974 and *Flanagan* 2586). These plants appear to have lacunae developed at the bases of the adaxial furrows between the bulliform cells and the mesophyll. These cavities are remarkably regular and consistent in size and occurrence and occur in association with all the furrows, particularly the lateral ones. These lacunae are lined by more or less disintegrated cells and surrounded by mesophyll tissue. It is possible that breakdown of the mesophyll brought about the formation of these lysigenous canals but another explanation is also possible. Unfortunately no plants with lacunae were freshly-fixed for this study and herbarium material only was examined. In the rehydration process it may have happened that the mesophyll cells became separated due to differential water uptake resulting in the appearance of these 'air canals'. It is felt that these actually are lacunae and that specimens with them may represent a segregate from the more southerly and westerly populations. These three plants are all very robust specimens with very long glumes and may actually be polyploids occurring in fresh water localities.

The most outstanding feature of the anatomy of *M. cincta* is the unique additional small vascular bundles located immediately below the first order vascular bundles in the massive adaxial ribs (Fig. 9) in all specimens examined except *Comins* 974. A single bundle only may occur below the first order bundle (Fig. 7) or a pair of additional bundles may be present alongside one another but at a lower plane than that of the first order bundles (Fig. 9). In other specimens three additional bundles are located at two different levels below the first order bundles. These extra bundles contain both phloem and protoxylem tissue (Fig. 9) and are always surrounded by an inner bundle sheath of thickened cells which may, or may not, be in direct contact with the abaxial part of the mestome sheath of the first order bundles. In addition a typical parenchyma sheath does not normally surround them entirely (Fig. 9) and they usually are completely embedded in the collenchyma tissue of the abaxial girders.

These fascinating bundles are unlikely to represent interconnecting transverse veins because in the eight specimens in which they were observed they were always sectioned in exactly the same plane as the normal vascular bundles. From this it can be reasonably inferred that at least throughout the middle part of the leaf lamina, these additional bundles lie parallel to the standard vasculature, that no actual fusion occurs with these bundles and they do not traverse the mesophyll or the hypodermal collenchyma. In some instances they lie in such close proximity to the first order vascular bundles that they may appear to be diverging from them but closer examination reveals that both bundles actually possess entire and discreet inner, mestome sheaths.

Vascular bundles inserted at different planes in the thickness of the leaf lamina are very rare in the Poaceae and are only generally encountered in the midribs and keels of the Bambuseae and Oryzeae. In these two tribes a complex vasculature is common with superposed, adaxial bundles being present near the adaxial epidermis and in the interior as well (Jacques-Felix, 1955; Schweickerdt & Marais, 1956; Metcalfe, 1960; Tateoka, 1963 and Launert, 1965). It is significant that in the bamboos and rices this complex system of vascular bundles is restricted to the midrib and keel only and that the vascular bundles are arranged in a single horizontal row along the width of the rest of the blade.

The only other grass in which the vascular bundles of the lamina have been reported to be in different planes is *Porteresia coarctata* (Roxb.) Tateoka (Tateoka, 1963, 1965). In this species each adaxial rib contains a single, small, superposed amphivasal bundle located above the typical first and third order bundles. In view of this unique feature, combined with differences in embryo anatomy and morphology, *P. coarctata* has been removed from *Oryza* and referred to the monotypic genus *Porteresia* (Tateoka, 1965).

The considerable taxonomic importance attached to the presence of the additional bundles in *Porteresia* has created a precedent and it seems appropriate to reconsider the classification of *M. cincta* in the light of this evidence. In *M. cincta* there are several differences in the structure and location of the additional bundles but both species agree in not having a midrib or keel. It is significant also that *M. cincta* does not have oryzoid silica bodies or arm cells in the mesophyll and, consequently, does not show any relationship with the Oryzoideae.

In the case of *M. cincta,* these unique vascular bundles do not seem to provide any clues as to the taxonomic relationships of *M. cincta.* They do, however, serve to emphasise that this species differs considerably in anatomical structure from the other *Merxmuellera* species (Ellis 1980; 1980a; 1981; 1981a and in press). Of the South African grasses anatomical resemblances between *M. cincta* and *Ammophila arenaria* of the Agrostideae have already been mentioned but similarities with some Australian danthonoid genera, such as *Chionochloa* and *Notadanthonia,* can be inferred from the illustrations of Clifford & Watson (1977). This observation is in agreement with the statement of Conert (1971) that there is no genus of African grasses to which *Merxmuellera* shows any relationship but that *Merxmuellera* agrees in certain characters with *Chionochloa* from New Zealand and *Cortaderia* from South America. *M. cincta* may, therefore, provide anatomical evidence for this relationship. This in turn raises problems with tribal definitions as *Merxmuellera* and *Chionochloa* are placed in the Danthonieae whereas *Cortaderia* is grouped with the Arundineae. The affinities of *M. cincta* are truly puzzling and will undoubtedly reward further investigation.

UITTREKSEL

Die anatomiese struktuur van die blaar in dwarssnee en die abaksiale epidermis, van Merxmuellera arundinacea *(Berg.) Conert en* M. cincta *(Nees) Conert word beskryf en geïllustreer. Hierdie twee spesies toon duidelike morfologiese ooreenkomste aan en is die enigste verteenwoordigers van die genus met oop, uitgespreide blare. Nietemin is hulle maklik onderskeibaar op anatomiese kenmerke, veral dié van die blaar in dwarssnee. Die anatomie van* M. cincta *is veral merkwaardig omdat dit addisionele vaatbondels besit wat reg onder die gewone vaatbondels geleë is. Hierdie vertikale rangskikking van vaatbondels op verskillende vlakke is 'n unieke eienskap van* M. cincta *en dui moontlik die behoefte aan vir taksonomiese regstelling.*

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Leaf anatomy of the South African Danthonieae (Poaceae). VII. *Merxmuellera dura* and *M. rangei*

R. P. ELLIS*

ABSTRACT

The leaf anatomy of *Merxmuellera dura* (Stapf) Conert and *M. rangei* (Pilg.) Conert is described and illustrated. These two species both occur in the arid, north-western parts of the winter-rainfall region, but they display differing anatomical adaptations to these harsh climatic conditions. *M. dura* has an infolded leaf blade with both adaxial and abaxial furrows and appears to form a link between the *M. disticha* (Nees) Conert group of species and the genus *Dregeochloa* Conert. Anatomical evidence suggests that *M. rangei* occupies an isolated taxonomic position and the cylindrical leaf blades of this species are unique in the genus.

INTRODUCTION

Merxmuellera dura (Stapf) Conert and *M. rangei* (Pilg.) Conert are two additional danthonoid species that have recently been removed from the genus *Danthonia* DC. and referred to the genus *Merxmuellera* Conert (Conert, 1970). Both these species have long been known to science, *M. dura* having been described in 1899 and *M. rangei* in 1909. However, *M. rangei* is unaccountably not mentioned in the standard reference to the South African grasses (Chippindall, 1955) although neither the status of this taxon nor the validity of the name seem to be in doubt. Therefore *M. rangei* is recognized by Conert (1970) and the name has been accepted by the National Herbarium, Pretoria (PRE) (Gibbs Russell & Smook, 1980).

M. dura and *M. rangei* are the two southern African *Merxmuellera* species that extend furtherest northward into the arid, north-western parts of the winter rainfall region of the Cape Province and South West Africa/Namibia. *M. dura* is found mainly in the Mountain Renosterbosveld and Western Mountain Karoo veld types but also occurs in the Arid Karoo. *M. rangei* is found even further to the north in the Lüderitz-Süd District of South West Africa/Namibia. It has been collected in the Aus area as well as further south between Witputz and Lorelei.

M. rangei appears to be restricted to dry, sandy habitats such as the plains between granite koppies and in dry water-courses. *M. dura* also occurs in sandy riverbeds or other habitats with accumulated fine, loose sand but, in addition, it appears to favour warm, dry rocky localities. Consequently it is also found on steep, north-facing, rocky, sandstone slopes. In this respect *M. dura* occupies a very similar niche to *M. arundinacea* albeit in a more northerly direction and their distributional ranges do not appear to overlap.

M. dura and *M. rangei* can be readily distinguished on morphological criteria and this distinction is further accentuated by the leaf anatomy. In the anatomical descriptions which follow, the following abbreviations will be used:

vb/s—vascular bundle/s
1'vb/s—first order vascular bundle/s
2'vb/s—second order vascular bundle/s
3'vb/s—third order vascular bundle/s
ibs—inner bundle sheath; mestome sheath
obs—outer bundle sheath; parenchyma sheath

ANATOMICAL DESCRIPTION OF *MERXMUELLERA DURA*

Leaf in transverse section

Leaf outline: reduced U-shaped (Figs 1 & 2) or elliptical (Fig. 3); channel width somewhat variable as leaf possesses limited ability to open and close; channel very deep and leaf width at median vb narrower than lateral parts. *Ribs and furrows:* adaxial furrows shallow, cleft-like and present between all vbs; adaxial ribs rounded with vertical sides and all of similar size. Abaxial ribs and furrows present; ribs flat-topped and separated by cleft-like furrows (Figs 1–3); present opposite all vbs. *Median vascular bundle:* smallest 1'vb in section. *Vascular bundle arrangement:* 7–9 1'vbs in section; 1 3'vb between successive 1'vbs; all vbs situated equidistant from abaxial and adaxial epidermides. *Vascular bundle structure:* all bundles elliptical; phloem without sclerified tissue; 3'vbs exhibit more phloem than xylem tissue. *Vascular bundle sheaths:* obs of 1' and 3'vbs similar in composition and structure; obs elliptical to tall and narrow; adaxial interruption slight; abaxial interruption slight to wide in 1'vbs; extensions consist of parenchyma cells on either side of sclerenchyma girders. Obs cells rounded and decrease in size along extensions; lack chloroplasts; slightly larger than mesophyll cells. Ibs complete in 1'vbs but reduced and opposite phloem only in 3'vbs; consist of heavily thickened cells with small lumens. *Sclerenchyma:* adaxial girders inversely anchor-shaped with very long, narrow stems; abaxial girders trapezoidal, narrowing towards vbs; consist of heavily thickened fibres. No sclerenchyma between bundles. *Mesophyll:* small, tightly-packed isodiametric cells in tall, elongated, X-shaped groups especially in freshly fixed material (Figs 1 & 2). No colourless cells present. *Adaxial epidermis:* no bulliform cells except at the bases of the two furrows on either side of the median vb; few elongated prickles on adaxial ribs. *Abaxial epidermis:* no bulliform cells even at bases of furrows; cuticle thick; no macro-hairs, prickles or papillae.

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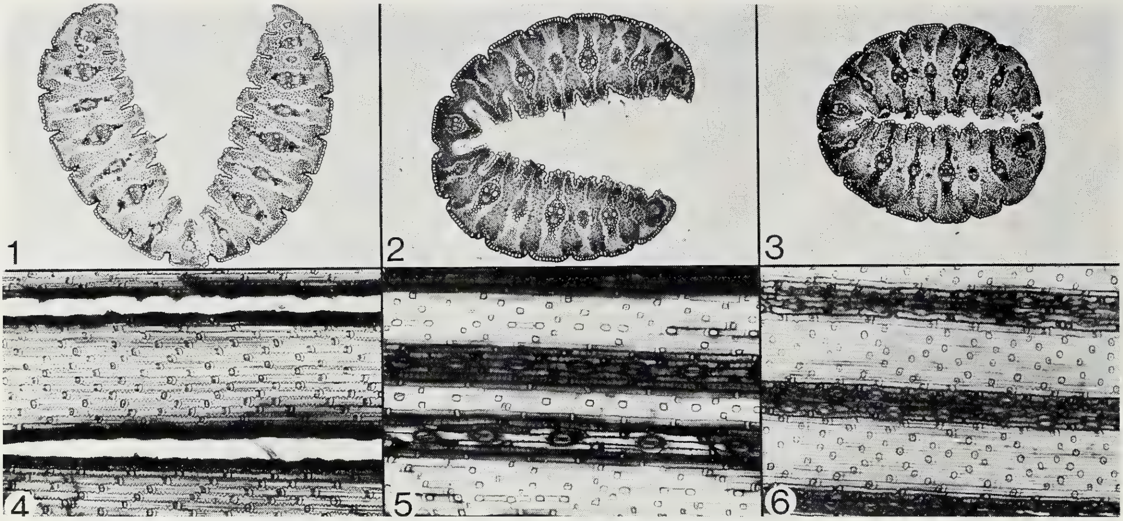


FIGS 1–6.—Leaf blade anatomy of *Merxmuellera dura*. 1–3, leaf blade outline in transverse section. All × 100. Note adaxial furrows. (1, *Ellis* 1719; 2, *Ellis* 2455; 3, *Ellis* 2465.) 4–6, abaxial epidermis in surface view. All × 250. (4, *Ellis* 2464; 5, *Ellis* 2455; 6, *Ellis* 2465.)

Abaxial epidermis

Intercostal zone: in form of stomatal groove and only visible on a few specimens (Figs 5 & 6). Intercostal long cells elongated, with parallel side walls and vertical end walls; walls slightly thickened and either straight or slightly undulating; no bulliform cells present. *Stomata:* if visible low dome-shaped; one or two rows per intercostal zone; successive stomata separated by single very elongated interstomatal cell (Fig. 5). *Intercostal short cells:* usually absent. Solitary, square with smooth walls if present. *Papillae:* absent. *Prickles:* usually not present; if present with medium bases and long barbs (Fig. 4). Present along margins of costal zones; overly stomatal groove. *Micro-hairs:* none seen. *Macro-hairs:* absent. *Silica bodies:* In specimens without stomata the silica bodies are tall and narrow, elliptical or cresent-shaped (Fig. 4) with closely associated cork cell. If stomata are present the bodies are rounded (Fig. 6) to oblong (Fig. 5) in shape without associated cork cells. Similar silica bodies present throughout costal zones; same width as costal long cells. *Costal cells:* silica cells or silica-suberose couples alternate with costal long cells with crenate walls (Fig. 4); adjacent costal files also alternate in the position of the silica cells.

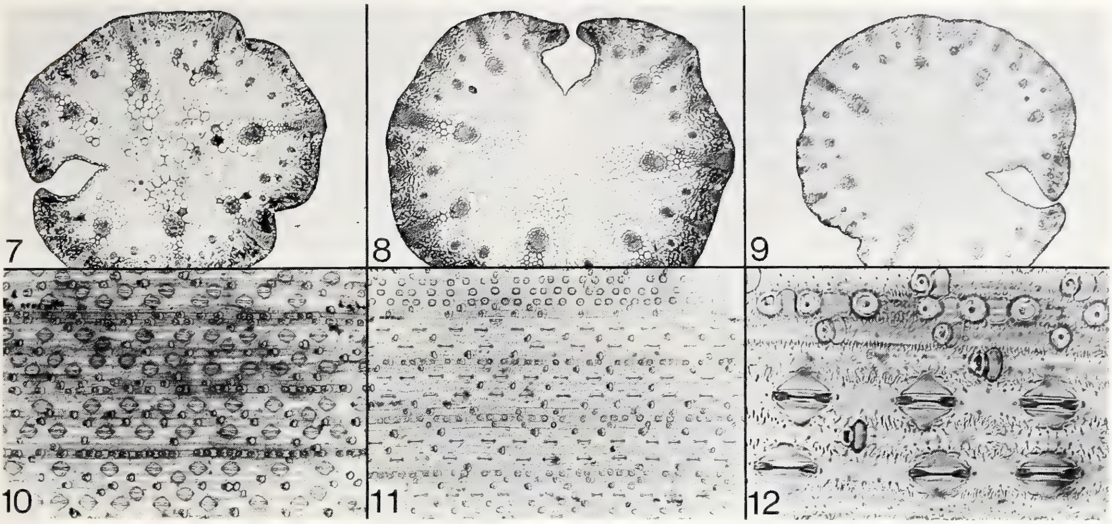
Specimens examined:

CAPE.—3119 (Calvinia): Nieuwoudtville (–AC), *Ellis 2455;* Hantam Mts (—BC), *Middlemost 2166;* Lokenburg (–CA), *Ellis 1719;* Perdefontein, Calvinia (–DD), *Acocks 17295.* 3220 (Sutherland): Middelpost (–AB), *Ellis 2464;* Sutherland (–BC), *Ellis 2465.*

ANATOMICAL DESCRIPTION OF *MERXMUELLERA RANGEI*

Leaf in transverse section

Outline of lamina: circular or rounded in section; solid cylinder with adaxial surface reduced to small groove (Figs 7—9). *Ribs and furrows:* absent on both surfaces; irregularities as in Fig. 7 probably due to inadequate rehydration of herbarium material. Tendency for slight abaxial undulations to be present opposite 1'vbs. *Median vascular bundle:* no keel or midrib developed. *Vascular bundle arrangement:* 7 1'vbs in leaf section; 1 3'vb between consecutive larger bundles and 1 2'vb between consecutive 1'vbs. 1'vbs centrally located in blade and 2' and 3'vbs abaxially situated (Fig. 8). *Vascular bundle description:* all vbs somewhat angular and elliptical in outline; xylem and phloem distinguishable. Protoxylem and metaxylem vessels of 1'vbs extremely narrow with diameters even less than those of the ibs cells. *Vascular bundle sheaths:* obs of 2' and 3'vbs circular to elliptical in shape; entire; no extensions. 1'vbs obs elliptical but with both adaxial and abaxial extensions. Adaxial extensions wide and merge gradually with the thin-walled colourless parenchyma cells of the interior of the leaf; more than 5 cells long. Abaxial extensions narrow and grade rapidly into conspicuous sclerenchyma strand. Obs cells with straight radial walls; cells large, inflated, conspicuous and considerably larger than the mesophyll cells; walls thicker than mesophyll cell walls; no chloroplasts. Ibs entire, comprised of very small cells irregularly thickened. *Sclerenchyma strands:* no adaxial sclerenchyma present; abaxial strands associated with 2' and 3'vbs; well-developed; as deep or deeper than wide as seen in transverse section; relatively narrow but deep girders associated with 1'vbs; narrower than the vbs; fibres thick-walled. *Mesophyll:* chlorenchyma irregularly arranged but somewhat pallisade-like in abaxial chlorenchyma; restricted to zone adjacent abaxial epidermis. Adaxial half of leaf consisting entirely of colourless cells; these are inflated, large, thin-walled parenchyma cells, regular in size; form pith-like tissue with uniform appearance (Figs 7–9). *Epidermal cells:* bulliform cells not present on either surface; no macro-hairs, papillae, hooks or prickles.



FIGS 7–12.—Leaf blade anatomy of *Merxmuellera rangei.* 7—9, transverse sections of the leaf blade. All × 100. Note cylindrical form with adaxial surface reduced to groove. (7, *Merxmüller & Giess* 28264; 8, *Schlieben* 11599; *De Winter & Giess* 6323.) 10–12, preparations of the abaxial epidermis. Note numerous stomata and narrow costal zones. (10, *De Winter & Giess* 6323, × 250; 11, *Merxmüller & Giess* 28264, × 250; 12, *Merxmüller & Giess* 28264, × 1000.)

Abaxial epidermis

Intercostal long cells: elongated, side walls parallel, end walls vertical, anticlinal walls heavily thickened and visibly pitted (Fig. 12); moderately to deeply sinuous; undulations U-shaped. Shape and size constant throughout all intercostal zones (Figs 10 & 11). No bulliform cells present. *Stomata:* triangular in shape with apices of subsidiary cells often evaginated (Fig. 12). Usually two, but sometimes three, rows of stomata per intercostal zone. Stomatal files separated by single file of long cells only (Fig. 12) or files with stomata adjoining (Fig. 10). Stomata present throughout intercostal zones. One interstomatal long cell between successive stomata (Fig 12); relatively short and much shorter than intercostal long cells. Stomata conspicuous and very numerous. *Intercostal short cells:* paired, silico-suberose couples with crescentic cork cell enfolding silica cell (Fig. 12); occur between most long cells. *Papillae:* absent. *Prickle hairs:* none seen. *Micro-hairs:* appear to be totally lacking. *Macro-hairs:* absent. *Silica bodies:* consistently round in shape; fitting into concavity of cork cell in intercostal zones; single silica cells or cork-silica cell pairs in costal zones (Fig. 12). Granules present. Costal cell arrangement variable.

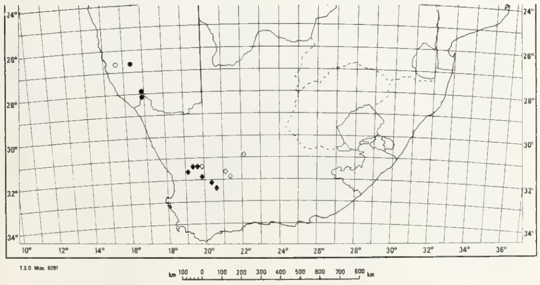


FIG. 13.—Distribution of *Merxmuellera dura* (◇) and *M. rangei* (○) compiled from specimens in the National Herbarium, Pretoria (PRE). Shaded symbols represent localities of specimens examined anatomically.

Specimens examined:

S.W.A.—2616 (Aus); (–CB), *Schlieben 11599,* 2716 (Witputz): Lüderitz-Süd (–DD), *Merxmüller & Geiss 28264.* 2816 (Oranjemund): Lorelei (–BB), *De Winter & Giess 6323.*

DISCUSSION AND CONCLUSIONS

Although *M. dura* and *M. rangei* both occur in the drier areas of the nothern parts of the winter-rainfall region (Fig. 13) they differ considerably in both anatomy and morphology. They are obviously not closely related and this study of the leaf anatomy accentuates the considerable differences that exist between these two species.

The leaf anatomy of *M. dura* conforms closely with that of most of the *Merxmuellera* species described previously (Ellis, 1980; 1980a; 1981; 1981a; 1982). Such attributes as vascular bundle and sheath structure, mesophyll composition and arrangement and epidermal structure are typical of the genus and are shared by *M. dura* and these other species. In the sequence of arrangement of the different orders of vascular bundle along the width of the blade *M. dura* resembles the '*M. disticha* type' with alternating first and third order bundles (Ellis, 1980; 1981a). This type of bundle arrangement has been described in *M. disticha* (Nees) Conert, *M. davyi* (C.E. Hubb.) Conert and *M. macowanii* (Stapf) Conert (Ellis, 1981a) and possibly also *M. arundinacea* (Berg.) Conert (Ellis, 1982). Anatomical indications are, therefore, that *M. dura* is a typical representative of the genus belonging to the *M. disticha* group of species.

This anatomical resemblance with the *M. disticha* group of species is most unexpected as morphologically *M. dura* closely resembles *M. stricta* (Schrad.) Conert and may easily be confused with one of the forms of this species (Chippindall, 1955). There is an overlap in panicle size and in the length of the awns of the lobes and the arrangement of the marginal hairs is not always clear. The only character that satisfactorily separates these two species is the glabrous or hairy condition of the lemma at the point of insertion of the central awn (Chippindall, 1955). *M. dura* is also usually more robust, with coarser, more rigid leaf blades and with a longer panicle. These two species are not easy to separate using morphological criteria and they appear to be closely related.

Anatomically *M. dura* and *M. stricta* can easily be distinguished. The most obvious difference being the presence of abaxial furrows between all the bundles in *M. dura* — a character it alone possesses amongst all the *Merxmuellera* species. This development of abaxial stomatal grooves is of interest because it is a feature present in two other danthonoid genera from these drier areas. This condition has already been described in *Dregeochloa* Conert (Ellis, 1977) and it also occurs in both species of *Asthenatherum* Nevski (Conert, 1962) and must be of adaptive significance in this hot, arid climate. The presence of abaxial stomatal grooves, is in marked contrast to the total absence of abaxial stomata in most *Merxmuellera* species from the mountainous areas to the east where rainfall is not a limiting factor. These abaxial furrows also possibly indicate a phylogenetic link between *M. dura* and *Dregeochloa,* although they differ in mesophyll structure and bulliform cell type and their generic separation is undoubtedly justified.

The supposed close relationship between *M. stricta* and *M. dura* is not confirmed by the anatomical evidence which appears to indicate a common origin with the *M. disticha* group of species. This inference is based primarily on the alternating sequence of first and third order bundles which is assumed to be a basic difference between two major groups within *Merxmuellera* (Ellis, 1981a). This assumption is based on evidence from the twelve summer rainfall *Merxmuellera* taxa and it is concluded that it is phylogenetically a significant difference. The situation in *M. dura,* however, seriously questions this deduction as, anatomically, *M. dura* and *M. stricta* also share many similarities apart from this difference in the arrangement of the different orders of vascular bundle. Epidermal structure of *M. dura* is similar to that of the specimens of the typical *M. stricta* type possessing abaxial stomata (Ellis, 1980a). The development of abaxial furrows is all that is required to result in almost identical epidermides. In addition, the typical form of *M. stricta* often has a single abaxial furrow on either side of the median vascular bundle (Ellis, 1980a) and is the only other species of this genus with this development. These apparent contradictions are impossible to explain at present and await further study particularly of the cytogenetics of *M. dura, M. stricta* and *M. disticha.*

The leaf anatomy of *M. rangei* is clearly distinct and differs drastically from that of all the other representatives of the genus. The presence of adaxial parenchyma and the consequent development of the solid, cylindrical leaf form is unique in this genus (Figs 7–9). The possession of three orders of vascular bundle and the parenchyma sheath cell size is also atypical for the genus. The leaf anatomy, therefore, indicates that *M. rangei* occupies an isolated position within the genus and possibly suggests that it warrants generic status as has been accorded *Dregeochloa pumila* (Nees) Conert which was previously classified in the genus *Danthonia* together with *M. rangei.* In common with *D. pumila, M. rangei* has adaxial colourless cell development (bulliform cells in the case of *D. pumila)* and mesophyll tissue that is not composed of tightly-packed, angular, isodiametric chlorenchyma cells. In all other respects these two species differ considerably and certainly do not seem to belong to the same genus. The leaf blade anatomy of *M. rangei* is obviously highly specialized and the taxonomic status that should be accorded the unique terete leaf form is uncertain.

The abaxial epidermal structure of *M. rangei* is worthy of comment. The exceptionally large number of unprotected stomata and the narrow costal zones (Figs 10–12) are difficult to explain in a grass where all other modifications tend to suggest a reduction in water loss. The cuticle of *M. rangei* appears to be thick as indicated by the pitted outer epidermal cell walls (Fig. 12) and perhaps this reduces water loss through these cells and it can only be assumed that the stomata themselves only open on limited occasions. The other danthonoid grasses from similar habitats all have well-protected stomata at the bases of deep furrows often densely overlaid by interlocking prickles. *M. stricta* is the only other *Merxmuellera* species possessing abaxial stomata (Ellis, 1980a) and the epidermis of these two species is remarkably similar in all respects except that *M. stricta* sometimes has micro-hairs — a feature not observed on *M. rangei.* This similarity in epidermal structure can possibly be interpreted as evidence that *M. rangei* is best placed in *Merxmuellera* and that the exceptional anatomical adaptations of the leaf in section are only of specific taxonomic importance.

UITTREKSEL

Die blaaranatomie van Merxmuellera dura *(Stapf) Conert en* M. rangei *(Pilg.) Conert word beskryf en geïllustreer. Hierdie twee spesies kom albei in die droë, noord-westelike dele van die winterreënval-streek voor maar die anatomiese aanpassings wat vertoon word verskil aansienlik.* M. dura *het 'n toegevoude blaar met beide adaksiale en abaksiale groewe en verteenwoordig dalk 'n binding tussen die* M. disticha *(Nees) Conert spesiesgroep en die genus* Dregeochloa *Conert. Anatomiese aanduidings dui daarop dat* M. rangei *'n geïsoleerde taxonomiese posisie beklee en die silindriese blare van hierdie gras is uniek in die genus.*

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Meiotic studies of some South African cultivars of *Lantana camara* (Verbenaceae)

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ABSTRACT

Lantana camara L. is a polyploid species with a basic chromosome number of 11 (x=11). Chromosome association in 39 cultivars indicated the occurrence of univalents to heptavalents with bivalents predominating. Multivalent association analysis revealed the presence in South Africa of at least four different groups of *L. camara* at the diploid level.

The potential for sexual reproduction must exist, at least at the diploid level, to account for differences in chromosomal behaviour that can only be attributed to hybridization. The possibility exists that the basic chromosome number may be lower than 11, or else postspeciation genomic evolution must have occurred. No cytogenetical correlation exists between the South African and Indian cultivars.

The number of chiasmata per genome increases with an increase in the polyploid level. Most multivalents are of the chain type. Univalents during diakinesis are the result of asynapsis. Triploid and pentaploid plants display a markedly abnormal meiosis. *L. camara* is a segmental allopolyploid species.

INTRODUCTION

Lantana camara L. is a widespread tropical weed noted for its toxicity to livestock and for its rapid invasion of natural pasturage, waste ground, forest margins and derelict or cultivated lands.

Experience gained from a number of areas of the tropics over many decades has shown that *L. camara* is not a homogeneous species, but actually consists of a number of forms. The origin, nature and spread of these forms have been discussed in the first paper of this series (Stirton, 1977).

L. camara is today recognized as a polyploid aggregate species with a basic chromosome number of x=11 and having diploid, triploid, tetraploid, pentaploid and hexaploid representatives (Schnack & Covas, 1947; Tjio, 1948; Singh, 1951; Sen & Sahni, 1955; Tandon & Bali, 1955; Tandon & Chandi, 1955; Natarajan & Ahuja, 1957; Henderson, 1969; Spies & Stirton, 1982). The need for an understanding of these different forms and their taxonomic relationships in South Africa prompted the biological control section of the Department of Agriculture and Fisheries to approach the Botanical Research Institute, of the same Department, to initiate a taxonomic study of *L. camara* in South Africa. This paper reports in depth on the value of meiotic analysis in circumscribing the more than 50 naturalized cultivars of the weed that are presently recognized in South Africa (Stirton & Spies, 1982).

MATERIALS AND METHODS

The plants used in this study are naturalized cultivars collected throughout South Africa and transplanted under quarantine in the Pretoria National Botanical Garden. Thirty-nine different cultivars, representative of all polyploid levels, were used in this study, 37 specimens being sampled from a hybrid swarm from the Transvaal lowveld.

Young inflorescences were collected between 09h00 and 12h00 hours and fixed for 24 hours in Carnoy's fixative. Anthers were then squashed in aceto-carmine (Darlington & La Cour, 1976). The multivalent configurations during diakinesis were emphasized for meiotic analysis.

RESULTS

The sample studied comprised 13 diploids, 12 triploids, 9 tetraploids, 3 pentaploids and 2 hexaploids (Table 1) and confirms our earlier report (Spies & Stirton, 1982) that *L. camara* in South Africa is a polyploid complex.

The early stages of meiosis were superficially similar in all the different cultivars although, during pachytene and diplotene, more chromosomes were visible in the higher polyploids (Fig. 1). Two chromosomes were always associated with the nucleolus at all polyploid levels.

Chromosome configurations during diakinesis ranged from univalents to heptavalents, but were predominantly bivalents (Fig. 2). The number of chiasmata during diakinesis, as well as the different configurations formed, are shown in Table 1. From Table 2 it can be deduced that there are big genome differences between different cultivars at the same polyploid level. These genome differences result in different chromosome associations.

A high frequency of unpaired chromosomes and laggards (Fig. 3) were encountered during anaphase I (Table 3). Secondary association of chromosomes during telophase I usually occurred (Fig. 4). Neither heteromorphic bivalents nor B-chromosomes were found.

Instead of studying metaphase II and anaphase II, we concentrated our attention on the number of micronuclei found during telophase II (Table 4). The triploids and pentaploids usually deviated from the expected 4 nuclei. The size and number of the additional nuclei varied significantly (Fig. 6).

In *Stirton* 7387, a triploid plant, chromatid segregation in two cells was noticed instead of chromosome segregation. No bridges were obser-

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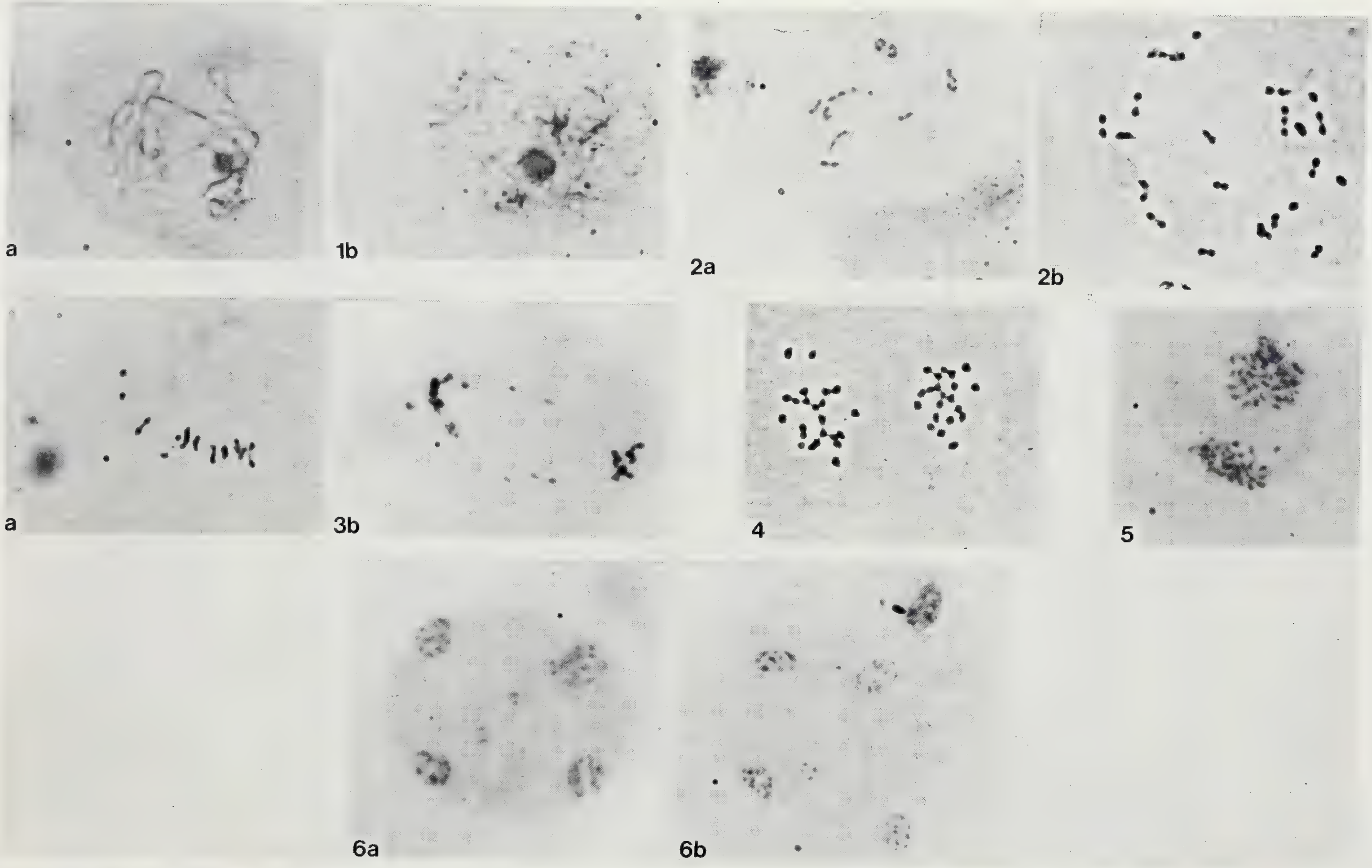

FIGS 1–6.—Meiosis in *Lantana camara*. 1, pachytene in a diploid (2n=22) (a), and a pentaploid (2n=55) (b) plant. 2, late diakinesis in a diploid (a), and tetraploid (b) plant. 3a, normal late metaphase I. 3b, anaphase I showing laggards as well as secondary association of chromosomes. 4, secondary association during telophase I. 5, telophase I in a 2n=33 plant; although chromosome counts are impossible, this is apparently a 33–33 segregation. 6a & b, telophase II showing additional micronuclei of various sizes.

TABLE 1. — Chromosome association, multivalent configuration types and chiasmata frequency in ***Lantana camara*** *during diakinesis. (All frequencies expressed as percentages.)*

Plant No. (Stirton)	2n=	No. of cells analysed	Chromosome association							Types of multivalent configurations																			Total No. of chiasmata/genome during diakinesis
										Bivalents				Trivalents			Quadrivalents					Petavalents				Hexavalents		Heptavalents	
			I	II	III	IV	V	VI	VII	Λ	X	ɣ	O	N	λ	ȯ	M	X	⊥	□	ɣ	W	ʅ	⌐X	⊐	ΛΛΛ	0	WW	
6882	22	25	0,36	99,64	–					41,61	40,15	12,77	5,47																6,48
7062	22	25	6,91	90,91	2,18					70,8	20,8	6,8	1,6	100															5,58
7066	22	25	–	100	–					61,82	29,09	6,91	2,18																6
7294	22	25	2,18	95,64	2,18					57,79	30,04	8,37	3,8	100															6.06
7304	22	25	4,55	93,82	1,64					60,85	29,84	–	9,3	100															5,76
7306	22	25	9,64	85,45	4,91					57,45	25,11	7,66	9,79	100															5,88
7311	22	25	9,82	89,09	1,09					71,02	26,53	–	2,45	100															5,1
7314	22	20	21,14	75,45	3,41					86,14	9,04	4,82	–	100															4,6
7315	22	20	18,41	75,45	6,14					65,66	20,48	9,04	4,82	100															5,18
7339	22	20	11,82	85,45	2,73					61,7	25	9,04	4,26	100															5,53
7361	22	20	10,68	88,64	0,68					71,79	22,56	3,59	2,05	100															5,2
7374	22	20	0,91	99,09	–					50	34,4	9,17	6,42																6,3
7389	22	20	5,45	93,18	1,36					74,63	14,15	11,22	–	100															5,8
x̄	22	22,69	7,83	90,14	2,02					63,92	25,17	6,88	4,01	100															5,65 ± 0,53
6878	33	20	10,45	58,18	31,36	–				60,42	18,75	14,58	6,25	71,01	28,99														6,17
6883	33	20	7,58	60,61	31,82	–				58	21	10,5	10,5	100	–														6,37
7067	33	20	7,73	72,73	19,55	–				64,17	15	12,5	8,33	100	–														6,27
7348	33	20	8,03	54,55	36,82	0,61				54,44	25,56	20	–	93,83	6,17		100												6,35
7381	33	20	3,79	83,94	12,27	–				57,4	22,74	13,36	6,5	100	–														6,43
7382	33	20	12,88	64,85	22,27	–				53,74	28,97	11,68	5,61	93,88	6,12														5,82
7383	33	20	8,94	73,64	16,82	0,61				52,26	34,16	4,53	9,05	86,49	13,51		100												5,88
7384	33	20	16,67	60,00	22,73	0,61				49,49	27,27	11,62	11,62	100	–		100												5,78
7387	33	20	8,18	65,45	26,36	–				61,11	22,22	14,81	1,85	100	–														6,13
7393	33	25	15,64	63,27	21,09	–				54,02	27,2	17,24	1,53	72,41	27,58														5,68
7394	33	25	14,3	50,42	35,27	–				61,54	15,38	15,38	7,69	100	–														6
7398	33	20	10,3	61,52	28,18	–				44,33	42,36	8,87	4,43	80,65	19,35														5,9
x̄	33	20,83	10,37	64,1	25,38	–				55,91	25,05	12,92	6,11	91,52	8,48														6,07 ± 0,26
5288	44	25	9	66,73	11,18	13,09	–	–		59,95	28,07	11,99	–	60,98	39,02		55,56	27,78	8,33	8,33	–								6,04
6784	44	20	8,07	58,18	13,3	20,45	–	–		89,84	7,81	–	2,34	58,97	41,03		91,11	–	–	8,89	–								5,99
7060	44	20	3,98	74,09	13,3	8,64	–	–		81,6	18,4	–	–	100	–		78,95	–	–	21,05	–								5,81
7087	44	20	9,77	58,64	17,05	14,55	–	–		52,33	47,67	–	–	100	–		100	–	–	–	–								5,65
7230	44	25	2,82	55,27	23,45	17,09	1,36	–		67,43	22,04	5,26	5,26	67,44	32,56		36,17	–	14,89	34,04	14,89	33,33	–	–	66,67				6,82
7253	44	20	5,34	72,27	16,02	6,36	–	–		97,17	2,83	–	–	100	–		85,71	–	–	14,29	–								5,7
7270	44	20	4,43	67,05	18,07	10,45	–	–		74,24	21,02	4,75	–	75,47	24,53		56,52	13,04	13,04	17,39	–								6,05
7312	44	25	4,45	63,09	11,73	20,73	–	–		70,61	17,58	9,8	2,02	79,07	20,93		63,16	12,28	–	24,56	–								6,61
7351	44	25	1,64	82,18	3,27	12,36	–	0,55		60,62	31,86	7,52	–	50	50		67,65	–	11,76	20,59	–						100		6,25
x̄	44	22,22	5,5	66,39	14,15	13,75	0,15	0,06		72,64	21,92	4,37	1,07	76,88	23,12		70,54	5,9	5,34	16,57	1,65	33,33			66,67		100		6,1 ± 0,48
5287	55	20	7,09	58,73	18,55	15,64	–			88,54	11,45	–	–	100			74,42	25,58	–	–	–								5,89
7430	55	20	6,73	40,91	18,82	25,82	7,73			57,78	17,78	16,44	8	100			66,2	33,8	–	–	–	64,71	–	35,29					6,99
7432	55	20	4,82	55,09	18	15,27	6,82			67,66	32,34	–	–	100			26,19	50	–	23,81	–	53,33	46,67	–					6,32
x̄	55	20	6,21	51,58	18,46	18,91	4,85			71,33	20,52	5,48	2,67	100			55,6	36,46	–	7,94	–	59,02	23,34	17,65					6,4 ± 0,55
7058	66	20	7,73	48,03	21,14	10,61	6,06	5,91	0,53	88,33	11,67	–	–	66,67	26,88	6,45	42,86	57,14	–	–	–	81,25	18,75			76,92	23,08	100	6,28
7431	66	20	7,73	44,7	12,95	30,3	1,52	2,27	0,53	65,42	20,68	13,9	–	100	–	–	70	10	–	20	–	100	–			100	–		6,81
x̄	66	20	7,73	46,37	17,05	20,46	3,79	4,09	0,53	76,88	16,18	6,95	–	83,34	13,44	3,23	56,43	33,57	–	10	–	90,63	9,38			88,46	11,54	100	6,57 ± 0,37

TABLE 2. — Multivalent associations in *Lantana camara*

ASSOCIATION	% ASSOCIATIONS/PLANT												
(a) The diploid group													
	6882	7062	7066	7294	7304	7306	7311	7314	7315	7339	7361	7374	7389
11II	96	32	100	72	64	28	48	-	20	30	35	90	50
10II 2I	4	40	-	12	16	28	20	10	-	30	25	10	25
9II 4I	-	12	-	-	12	8	8	35	20	10	15	-	15
9II 1I 1III	-	12	-	12	4	12	-	5	-	-	5	-	10
8II 6I	-	-	-	-	-	-	16	15	15	5	20	-	-
8II 3I 1III	-	4	-	4	-	8	-	10	10	10	-	-	-
7II 8I	-	-	-	-	-	-	-	10	-	5	-	-	-
7II 5I 1III	-	-	-	-	-	12	4	10	20	5	-	-	-
6II 10I	-	-	-	-	-	-	-	5	-	-	-	-	-
6II 7I 1III	-	-	-	-	-	4	4	-	15	5	-	-	-
6II 4I 2III	-	-	-	-	4	-	-	-	-	-	-	-	-

(b) The triplo.   group

	6878	6883	7067	7348	7381	7382	7383	7384	7387	7393	7394	7398
16II 1I	-	-	5	-	-	-	-	-	-	-	-	-
15II 1III	-	-	5	-	40	-	20	-	-	-	-	-
15II 3I	-	-	5	-	-	-	-	-	-	-	-	-
14II 2I 1III	-	-	-	-	15	-	5	-	-	12	-	-
14II 5I	-	-	10	-	-	-	-	-	-	-	-	-
13II 1I 2III	-	10	15	15	25	10	30	-	15	4	4	-
13II 4I 1III	-	-	-	-	15	5	20	10	-	-	-	-
12II 3III	-	-	-	-	-	-	-	-	-	4	4	-
12II 3I 2III	-	-	5	-	-	25	-	-	20	12	12	20
12II 6I 1III	-	-	-	-	-	-	-	-	-	4	4	-
11II 2I 3III	-	20	30	10	5	-	5	5	25	8	4	-
11II 5I 2III	15	-	-	-	-	25	-	20	-	8	4	15
11II 8I 1III	-	-	-	-	-	-	-	5	-	-	-	-
10II 1I 4III	5	10	-	-	-	-	-	-	-	-	-	-
10II 4I 3III	30	15	20	-	-	-	5	15	5	12	8	40
10II 7I 2III	-	-	-	-	-	10	-	5	5	-	-	-
10II 13I	-	-	-	-	-	-	-	-	-	16	8	-
9II 3I 4III	45	40	5	35	-	-	-	5	30	-	-	15
9II 6I 3III	-	-	-	15	-	10	-	10	-	-	-	10
8II 2I 5III	5	5	-	-	-	5	-	-	-	-	-	-
8II 8I 3III	-	-	-	-	-	-	-	20	-	-	4	-
7II 1I 6III	-	-	-	-	-	5	-	-	-	-	-	-
7II 5III 1IV	-	-	-	5	-	-	-	-	-	-	-	-
7II 7I 4III	-	-	-	-	-	-	-	-	-	8	-	-
7II 10I 3III	-	-	-	-	-	5	-	-	-	-	-	-
7II 6I 3III 1IV	-	-	-	-	-	-	-	5	-	-	-	-
7II 15I 1IV	-	-	-	-	-	-	5	-	-	-	-	-
6II 7III	-	-	-	10	-	-	-	-	-	-	-	-
6II 3I 6III	-	-	-	-	-	-	-	-	-	4	8	-
6II 6I 5III	-	-	-	-	-	-	5	-	-	8	12	-
5II 2I 7III	-	-	-	5	-	-	-	-	-	-	16	-
5II 5I 6III	-	-	-	5	-	-	-	-	-	-	4	-
5II 8I 5III	-	-	-	-	-	-	5	-	-	-	8	

(c) The tetraploid group

	5288	6784	7060	7087	7230	7253	7270	7312	7351
21II 2I	-	-	-	-	-	-	-	-	4
20II 1I 1III	-	-	5	5	-	15	-	-	40
19II 2I 1IV	4	-	-	-	-	-	-	-	12
19II 3I 1III	-	-	10	-	-	-	-	-	-
18II 5I 1III	-	-	-	-	-	-	-	-	-
18II 4I 1IV	4	-	-	-	-	-	-	-	-
18II 2I 2III	-	-	10	-	-	30	-	-	-
18II 1I 1III 1IV	4	-	-	-	-	10	-	-	-
17II 4I 2III	-	-	-	-	-	-	-	12	-
17II 3I 1III 1IV	-	-	5	-	-	-	-	-	-
17II 2I 2IV	4	-	-	-	-	-	-	-	-
17II 1I 3III	-	-	5	-	-	-	-	-	-
16II 5I 1III 1IV	-	-	-	5	-	-	-	-	-
16II 3I 3III	-	-	-	5	-	-	15	-	-
16II 2I 2III 1IV	-	-	30	10	-	-	-	-	-
16II 4III	-	-	-	-	-	-	10	-	-
16II 3IV	-	-	-	-	-	-	-	20	36
15II 7I 1III 1IV	8	-	-	-	-	-	-	-	-
15II 5I 3III	-	-	-	-	4	-	-	-	-
15II 4I 2III 1IV	24	10	-	5	-	-	10	-	-
15II 3I 1III 2IV	24	-	-	-	-	-	-	4	-
15II 2I 4III	-	-	-	-	16	-	-	-	-
15II 1I 3III 1IV	-	-	10	-	-	-	15	12	-
15II 2III 2IV	-	-	10	-	-	-	5	-	4
15II 2IV 1VI	-	-	-	-	-	-	-	-	4
14II 6I 2III 1IV	-	10	-	-	-	-	-	-	-
14II 4I 3IV	-	5	-	-	-	-	-	-	-
14II 3I 3III 1IV	-	-	-	-	-	-	5	4	-
14II 2I 2III 2IV	4	5	15	-	8	-	35	-	-
14II 4III 1IV	-	-	-	-	-	10	-	-	-
13II 5I 3III 1IV	12	-	-	5	-	-	-	-	-
13II 4I 2III 2IV	-	-	-	5	-	10	-	-	-
13II 3I 5III	-	-	-	-	-	5	-	-	-
13II 2I 4III 1IV	-	-	-	5	-	-	5	-	-
13II 2I 4IV	-	25	-	-	-	-	-	-	-
13II 1I 3III 2IV	-	15	-	10	16	-	-	-	-
13II 2III 3IV	-	-	-	5	-	-	-	-	-
12II 9I 1III 2IV	-	-	-	5	-	-	-	-	-
12II 7I 3III 1IV	-	-	-	10	-	-	-	-	-
12II 6I 2III 2IV	-	-	-	-	-	-	-	4	-
12II 5I 5III	-	10	-	-	-	-	-	-	-
12II 3I 3III 2IV	8	10	-	-	8	15	-	-	-
12II 2I 2III 3IV	-	-	-	-	-	-	-	40	-
12II 1I 2III 2IV 1V	-	-	-	-	4	-	-	-	-
12II 4III 2IV	-	-	-	-	12		-	-	-
11II 9I 3III 1IV	-	-	-	5	-	-	-	-	-
10II 4III 3IV	-	-			- -				
9II 2I 4III 3IV	-	-	-	5	-	-	-	-	-
9II 3III 3IV 1V	-	-	-	-	4	-	-	-	-
8II 11I 3III 2IV	4	5	-	-	-	-	-	-	-
8II 8I 4III 2IV	-	-	-	5	-	-	-	-	-
8II 3I 4III 2IV 1V	-	-	-	-	4	-	-	-	-
6II 11I 3III 3IV	-	-	-	5	-	-	-	-	-

(d) The pentaploid group	5287	7430	7432
20II 2I 3III 1IV	15	-	-
18II 1I 2III 3IV	-	20	-
17II 4I 3III 2IV	30	-	-
17II 2I 5III 1IV	-	-	30
17II 1I 1III 3IV 1V	-	-	20
16II 5I 2III 3IV	5	-	-
16II 3I 4III 2IV	15	-	-
16II 2I 3III 3IV	-	5	-
16II 1I 6III 1IV	20	-	-
16II 1I 3III 2IV 1V	-	-	5
15II 4I 3III 3IV	-	-	5
15II 3I 3III 2IV 1V	-	-	15
15II 3I 2III 4IV	-	5	-
15II 2I 1III 5IV	-	-	5
14II 5I 3III 2IV 1V	-	-	5
14II 3I 4III 3IV	-	15	-
14II 2I 3III 4IV	-	10	-
11II 10I 1III 5IV	15	-	-
11II 3I 3III 4IV 1V	-	5	-
10II 5I 7III 1IV 1V	-	-	5
10II 3I 3III 2IV 3V	-	-	5
8II 8I 3III 3IV 2V	-	-	5
7II 8I 5III 2IV 2V	-	15	-
4II 5I 4III 5IV 2V	-	25	-

(e) The hexaploid group	7058	7431
22II 7I 2III 1IV 1V	5	-
20II 3I 5III 2IV	5	-
19II 4I 5III 1IV 1V	-	5
19II 1I 6III 1IV 1V	25	-
18II 4I 4III 2IV 1VI	5	-
17II 7I 3III 4IV	-	5
17II 4I 4III 4IV	-	5
16II 5I 5III 2IV 1VI	15	-
16II 5I 3III 5IV		10
16II 3I 7III 1IV 1VI	-	5
16II 3I 4III 2IV 1V 1VI	5	-
15II 5I 2III 5IV 1V	-	5
15II 4I 4III 5IV	5	10
14II 7I 1III 7IV	-	10
14II 5I 3III 6IV	-	20
14II 2I 7III 1IV 1V 1VI	5	-
14II 6III 1IV 2V 1VI	5	-
13II 6I 2III 7IV	-	15
13II 6I 1III 5IV 1V 1VI	-	5
13II 3I 4III 2IV 1V 2VI	5	-
13II 3I 1III 1IV 1V 3VI 1VII	-	5
11II 16I 3III 2IV 1V 1VI	5	-
11II 11I 3III 2IV 2V 1VI	5	-
10II 18I 3III 2IV 1V 1VI	5	-
10II 11I 3III 2IV 1V 1VI 1VII	5	-

The results of this study indicate that at least three genomes, of which two are at least partially homologous and the third is nonhomologous to either of them, could have contributed to the development of *L. camara.*

The frequency of trivalents is too high and the rate of haplodization too low for secondary haplodization to play any major part in this case of speciation.

In the third case, minor genomic differences exist in different cultivars of *L. camara.* These differences could be the results of prespeciation differences (described above) or post-speciation genomic evolution in the form of translocations, inversions, duplications and deletions. In order to determine which process actually occurred, a study of chromosome morphology is absolutely essential. In either case, however, hybrids between cultivars with minor differences in genomes, will result in a group of diploid plants with different chromosomal behaviour to that encountered in this South African hybrid swarm.

The occurrence of lower basic chromosome numbers in the Verbenaceae (x=5,6 and 7) (Lewis & Oliver, 1961), supports the theory of a possible lower basic chromosome number for *L. camara.* Further support for this theory might be the occurrence of 12 as a basic chromosome number in other species of *Lantana,* where different compositions from the low basic numbers are responsible for this difference rather than aneuploidy at the higher chromosome level.

Contrary to the findings of this study Natarajan & Ahuja (1957) found no evidence at any polyploid level for a basic chromosome number lower than 11. This clearly indicates that either post introduction genomic evolution occurred in either group or that totally different cultivars of *L. camara* were introduced into South Africa and India respectively.

b) *The triploid group*

Univalents, bivalents, trivalents and an occasional tetravalent (0,15%), were encountered during diakinesis (Table 1). Most chromosome configurations were bivalents (64,1%) followed by trivalents (25,38%). Multivalent association analysis revealed 33 different types of chromosome associations in triploid *L. camara* plants (Table 2). Five association types, $13_{11}\ 1_{1}\ 2_{111}$ (9,76%), $12_{11}\ 3_{1}\ 2_{111}$ (8,13%), $11_{11}\ 2_{1}\ 3_{111}$ (9,35%), $10_{11}\ 4_{1}\ 3_{111}$ (12,6%) and $9_{11}\ 3_{1}\ 4_{111}$ (14,23%), occurred in 54,07% of all cells studied.

TABLE 3.—Chromosome segregation during anaphase I

Chromosome Distribution	% OF CELLS IN EACH DISTRIBUTION TYPE												
(a) The diploid group	6882	7062	7066	7294	7304	7306	7311	8314	7315	7339	7361	7374	7389
12—8—2	—	—	—	—	—	—	—	—	—	10	—	—	—
11—11	100	100	100	60	90	90	100	100	90	90	100	100	100
11—10—1	—	—	—	10	—	—	—	—	—	—	—	—	—
11—9—2	—	—	—	30	—	—	—	—	—	—	—	—	—
11—7—4	—	—	—	—	—	—	—	—	10	—	—	—	—
10—9—3	—	—	—	—	10	—	—	—	—	—	—	—	—
10—8—4	—	—	—	—	—	10	—	—	—	—	—	—	—
(b) The triploid group	6883	7067	7381	7382	7383	7384	7387	7393	7394	7398			
33—33	—	—	—	—	—	—	10	—	—	—			
20—13	—	—	4,17	—	5	—	—	—	—	5			
19—14	—	—	—	9,52	—	—	—	5	5	—			
19—12—2	10	—	—	—	5	—	—	—	10	5			
18—15	25	—	4,17	19,05	20	35	20	50	50	30			
18—13—2	15	—	—	—	5	—	—	10	15	10			
17—16	20	35	8,33	14,29	20	35	20	30	10	15			
17—15—1	—	30	—	—	—	—	20	—	—	—			
17—14—2	—	20	—	—	—	—	15	—	—	—			
17—12—4	10	—	—	4,76	—	—	—	—	10	15			
16—16—1	—	—	—	—	—	—	15	—	—	5			
16—15—2	10	10	12,5	9,52	10	—	—	—	—	—			
16—14—3	—	5	4,17	—	5	—	—	—	—	—			
16—13—4	—	—	—	4,76	—	—	—	—	—	5			
15—15—3	5	—	16,67	9,52	10	—	—	—	—	—			
15—14—4	—	—	25	14,29	10	—	—	—	—	—			
14—14—5	—	—	25	14,29	10	—	—	—	—	—			
14—13—6	—	—	—	—	—	10	—	5	—	5			
13—12—8	5	—	—	—	—	10	—	—	—	—			
12—11—10	—	—	—	—	—	5	—	—	—	5			
11—11—11	—	—	—	—	—	5	—	—	—	—			
(c) The pentaploid group	7432												
30—23—2	25												
26—26—3	20												
25—25—5	5												
25—20—10	10												
24—24—7	30												
24—23—8	10												

TABLE 4.—The number of micronuclei per cell during telophase II. (Percentage of cells within each class.)

Stirton No.	Normal (4 nuclei)	4 + 1	4 + 2	4 + 3	4 + 4	4 + 5	4 + 6
(a) Diploids							
6882	100						
7062	100						
7066	100						
7294	90	10					
7304	100						
7306	100						
7311	100						
7314	100						
7315	100						
7339	90	10					
7361	100						
7374	100						
7389	100						
(b) Triploids							
6878	10	50	20	20			
6883	5	35	45	5	5	5	
7067	50	40	10				
7348	10	30	50	10			
7381		20	30	40	10		
7382	10	30	30	20	10		
7383	10	20	10	30	20	10	
7384	20	50	30				
7387	20	30	40	10			
7393	20	30	30	10	10		
7394	10	20	10	40	10		10
7398		60	30	10			
(c) Tetraploids							
5288	100						
6784	100						
7060	100						
7087	100						
7230	100						
(d) Pentaploids							
5287	10	20	20	40	10		
7430	20	20	30	30			
7432	20	40	30	10			
(e) Hexaploids							
7058	80	20					
7431	90	10					

The frequency of trivalents indicates allopolyploidy with *Stirton* 7348 & 7394 tending towards autopolyploidy and *Stirton* 7381 & 7383 tending towards allopolyploidy. The remainder of the plants were distributed between these extremes.

The chromosome association pattern encountered during this study differs significantly from the results obtained by Natarajan & Ahuja (1957). About half their number of trivalents and twice their number of bivalents were found in this study. This clearly indicates that the Indian material differs quite considerably from the South African material. Where the Indian material might represent autotriploid plants, the South African plants are definitely segmental alloploids. Whereas the South African material suggests a basic chromosome number lower than 11 (more than 11 bivalents and trivalents are present), the Indian plants give no indication of a basic chromosome number lower than 11 (Natarajan & Ahuja, 1957).

A high frequency of univalents was encountered. In addition to the univalents resulting from asynapsis, univalents are expected in triploid plants when bivalents are formed. The higher chromosome number produced more homologue chromosomes in the triploid compared with the diploid plants, so the role of asynapsis was diminished. The formation of quadrivalents is insignificant.

Very little variation (s=0,26) in the number of chiasmata formed was encountered. The number of terminal one chiasma bivalent configurations is lower in the triploid than in the diploid group. The number of terminal two chiasmata bivalents and terminal-subterminal two chiasmata bivalents is almost doubled. This led to a considerable increase in the number of chiasmata per genome compared to the diploids.

In addition to the chain type trivalents, a star type trivalent was encountered in 8,48% of the trivalents formed. This indicates that two chiasmata can occur close to each other, since this type of configuration requires a terminal chiasma between two chromosomes and a subterminal chiasma between one of them and another chromosome. All quadrivalents were of the chain type.

Anaphase I revealed vast differences between the triploid plants. In most of the cells studied a 18−15 (25%) or 17−16 (20,5%) distribution was found. One cell of *Stirton* 7384 acted as an allotriploid plant should, resulting in a 11-11-11 distribution. The other cells studied contradicted this observation.

In two cells of another plant (*Stirton* 7387) chromatid segregation occurred during anaphase I. If these cells had reached maturity, they would have had triploid pollen with the potential to increase the polyploid level of *L. camara* once again.

The abnormal anaphase I is reflected in an irregular second division. Only 30,08% telophase II cells had the expected 4 nuclei. As this does not guarantee that all the normal telophase II cells will develop into fertile pollen, the South African triploid *L. camara* will have less fertile pollen than their Indian counterparts (Tandon & Bali, 1955).

In both South African and Indian material an irregular meiosis was observed (Khoshoo & Mahal, 1967). Whereas the South African material mostly had a high number (more than 11) of bivalents, the Indian material had mostly 3_{111} 6_{11} 12_{1} (Tandon Bali, 1955) associations. The occurrence of more than 11 bivalents and trivalents in the South African material indicates homology between more than two genomes, therefore a basic chromosome number of less than 11 seems possible.

c) *The tetraploid group*

The tetraploid plants were a heterogeneous group (Table 1). The group had mostly bivalents, followed by trivalents, quadrivalents, univalents, a few pentavalents and even a hexavalent. Within the group large differences were encountered. The number of bivalents formed varied from 55,27% in *Stirton* 7230 to 82,8% in *Stirton* 7351. No evidence of a allotetraploid-like *L. camara* var. *mista* Bailey with only bivalents (reported by Natarajan & Ahuja, 1957) was found.

Whereas *Stirton* 6784, 7312 & 7351 had significantly more quadrivalents than trivalents, *Stirton* 7060, 7230, 7253 & 7270 had significantly less quadrivalents than trivalents. *Stirton* 5288 and 7087 were intermediate between these groups. Although this finding may appear to indicate three groups, the cytogenetical differences between the plants in each 'group' are too large to group them together.

During this study a much lower incidence of univalents and a higher number of bivalents was encountered than Natarajan & Ahuja (1957) reported.

The high frequency of multivalents indicates a segmental alloploid origin with an inclination towards autopolyploidy. Slightly more chiasmata per genome were encountered in the tetraploid group than in the triploids (Table 1). A very high frequency (72,64%) of terminal one chiasma bivalents were formed. The trivalents were mostly of the chain type with a significant increase in the number of the star types (23,12%). Five different quadrivalent types were encountered. Usually the chain type (70,54%) and a ring of four (16,57%) were seen. The other types included a star (5,9%), a T (5,34%), and a terminal bivalent ring associated with a terminal bivalent chain (1,65%), to form a quadrivalent.

Pentavalents were encountered in one plant (*Stirton* 7230). The pentavalent consisted of a chain (33,333%) or of a ring of four with one chromosome associated in a near terminal chiasma with the ring. The hexavalent was in the form of a ring.

The few anaphase I cells suitable for analysis seemed to be normal. Telophase II was normal with four nuclei:

d) *The pentaploid group*

Unfortunately only three pentaploid plants were encountered during this study. Multivalent association analysis indicated that these plants are totally different. The differences are evident in every cytogenetic aspect examined.

One plant (*Stirton* 5287) had no pentavalents, and the other two plants had 7,73% and 6,82% pentavalents respectively. The number of univalents (6,21%) is much lower than expected after studying the triploid group (10,37%). The high chromosome number obtained by segmental allopolyploidy could have increased the number of homologue chromosomes to rule out asynapsis at the higher polyploid levels.

The total number of chiasmata per genome differs from 5,89 to 6,99. Bivalents were usually of the chain type with terminal chiasmata. Only *Stirton* 7430 had bivalents with two chiasmata. All trivalents were of the chain type. With the exception of *Stirton* 7432, quadrivalents were usually of the chain type with approximately a quarter of all quadrivalents of the star type. In *Stirton* 7432 half the quadrivalents were of the star type with an equal amount of chains and rings. Pentavalents were usually of the chain type, followed by a T-type and an elongated star type.

Anaphase I was observed in *Stirton* 7432 only and it seemed to be quite irregular with between 2 and 10 laggards. Irregular meioses in pentaploid *L. camara* plants were also described by Khoshoo & Mahal (1967). Telophase II revealed an irregular meiosis with 4 nuclei in only 16,7% of the cells studied.

e) *The hexaploid group*

Only two plants were found and studied. In almost all cytogenetical aspects these two plants differ. No correlation could be found by multivalent association analysis. The same number of multivalents are formed in each plant but the frequencies of the different multivalent configurations varies significantly. The figures obtained during this study correspond well with Natarajan & Ahuja's (1957) figures, except for the number of quadrivalents where twice their number was observed.

No terminal bivalent rings were found. Trivalents consisted usually of chains (83,34%) and stars (13,44%), but a terminal bivalent ring associated with a near terminal chiasma to another chromosome was found in 6,45% of the trivalents. Quadrivalents occurred mainly as chains (56,43%) and stars (33,54%) with an occasional ring (10%). Pentavalents were found as chains (90,63%) and T's (9,38%). The hexavalents had chains (89,46%) and rings (11,54%) while all heptavalents were chains.

Anaphase I seemed normal and an extra micronucleus was encountered in only one telophase II cell (Table 4).

CONCLUSIONS

L. camara is a polyploid species. Since all polyploid forms encountered are multiples of 11 this number has been considered to be the basic chromosome number. The results of this study indicate either a lower basic chromosome number than 11, or postspeciation evolution of the genome must have occurred.

Cytogenetical differences at all polyploid levels indicate the occurrence of different genomic compositions in *L. camara*. This indicates either the introduction of different cultivars followed by hybridization in the past or a high rate of post introduction evolution has occurred within this species. At the diploid level at least four different groups exist with signs of hybridization.

The South African and Indian cultivars of *L. camara* reveal quite different chromosomal behaviour, implying that either different cultivars were introduced into these countries, or post introduction evolution in both countries resulted in different cultivar assemblages.

The polyploid forms of South African cultivars of *L. camara* are segmental allopolyploid plants.

UITTREKSEL

Lantana camara *L. is 'n poliploïede spesie met 'n basiese chromosoomgetal van 11 (x=11). Die chromosoom assosiasies van 39 kultivars het aangetoon dat monovalente tot heptavalente voorkom met hoofsaaklik bivalente. Multivalent assosiasie analise toon aan dat minstens vier verskillende diploïede* L. camara *groepe in Suid-Afrika voorkom.*

Geslagtelike voortplanting moet potensieel moontlik wees op diploïede vlak om verbastering moontlik te maak, aangesien slegs verbastering die waargenome verskille in chromosoomgedrag kan verklaar. Dit is moontlik dat die basiese chromosoomgetal laer as 11 is of dat genoom ewolusie na spesie vorming plaasgevind het. Geen sitogenetiese korrelasie bestaan tussen die Suid-Afrikaanse en Indiese kultivars nie.

Die aantal chiasmata per genoom vermeerder namate die poliploïede vlak styg. Meeste multivalente is van die ketting tipe. Monovalente gedurende diakinese kan aan asinapsis toegeskryf word. Triploïede en pentaploïede plante toon abnormale meioses. L. camara *is 'n segmentele allopoliploïed.*

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Embryo sac development in some South African cultivars of *Lantana camara*

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ABSTRACT

Twenty embryo sacs from each of 20 different *Lantana camara* L. cultivars naturalized in South Africa were examined. The normal sexual embryo sacs were monosporic 8-nucleated embryo sacs of the polygonum type and were encountered in 55% of the material examined. Several deviations from this pattern were recorded. Occasionally one of the nuclei failed to develop into a synergid, resulting in three polar nuclei.

Contrary to published information, the antipodal cells did not increase in size, nor was there an increase in the number of nuclei per cell. Although the occurrence of sexuality is confirmed, no definite evidence exists for the occurrence of apomixis. The occurrence of two embryo sacs per locule might be the result of either apospory or of sexuality whereby two embryo sacs were formed from two megaspores.

INTRODUCTION

Lantana camara L. is rated as one of the world's ten worst weeds (Holm & Herberger, 1969). This South American species is today recognized as a polyploid aggregate species (Stirton, 1977) and has recently been confirmed as such in South Africa (Spies & Stirton, 1982a).

Although some genetic studies of *L. camara* have suggested the occurrence of apomixis (Raghavan & Arora, 1960; Khoshoo & Mahal, 1967), this phenomenon has not been reported in any of the embryological studies done so far (Junell, 1934; Patermann, 1935; Tatachar, 1940; Padmanabhan, 1959; Kahleel & Nalini, 1972). We decided to investigate whether apomixis plays any role in the reproductive cycle of this successful weed in South Africa, because we have encountered over 40 different cultivars of *L. camara* with variable seedset.

MATERIALS AND METHODS

The plants used in this study are naturalized cultivars collected from throughout South Africa and transplanted in the Pretoria National Botanical Garden. This material has been studied cytogenetically (Spies & Stirton, 1982b) and taxonomically (Stirton & Spies, 1982). The research material has consequently been chosen carefully within each polyploid level and is representative of plants with normal and abnormal meiosis.

Young inflorescences were collected and fixed at 4°C for at least 24 hours in Navashin fixative (Stockholm modification, Maheshwari, 1939). The material was then washed in running tap water and serially dehydrated in ethyl alcohol and tertiary butyl alcohol. Tissue Prep (T565) was used as an embedding agent. The 9–12 micron sections were stained in Safranin and Fast Green (Johansen, 1940 — with minor modifications).

Twenty different embryo sacs from each plant were examined to determine the percentage of normal sexual embryo sacs.

RESULTS

L. camara has a bilocular ovary with a single anatropous ovule in each locule. The nucellus is one cell layer thick and is surrounded by a single massive integument. The archesporium is hypodermal and functions directly as megaspore mother cell (Fig. 1).

Meiotic cell divisions result in a linear tetrad of megaspores, of which only the chalazal one is usually functional (Fig. 2). Normally the development of the megaspore into an embryo sac causes degeneration of the other three megaspores. The non-functional megaspore of *L. camara* are mostly persistent (Fig. 10). The functional megaspore undergoes mitosis producing two daughter-nuclei (Fig. 3) that are subsequently separated to opposite poles by the formation of a central vacuole (Fig. 4). Each nucleus divides twice, resulting in an eight-nucleated embryo sac (Fig. 5 and 6).

The mature embryo sac is broader in the micropylar region and tapers towards the chalazal pole. The egg apparatus consists of two synergids and an egg. In the centre of the embryo sac there are two adjacent polar nuclei with three antipodal cells at the chalazal pole. This pattern was found in 54,75% of the embryo sacs studied (Table 1).

The most common deviation from this generalized pattern was the occurrence of two embryo sacs in each locule. In these cases the embryo sacs are always located at the polar ends of the locule (Fig. 7), with only a slight overlap occurring in the equatorial region. This pattern was found in 42,5% of the embryo sacs studied.

In the remaining 2,75% of embryo sacs examined, there was a maldistribution of the nuclei. In ten embryo sacs one of the synergids moved with the polar nucleus towards the equatorial region. In these cases, the egg apparatus consisted of an egg and only a single synergid (Fig. 8). Finally, we found a single embryo sac with twenty antipodal nuclei (Fig. 9).

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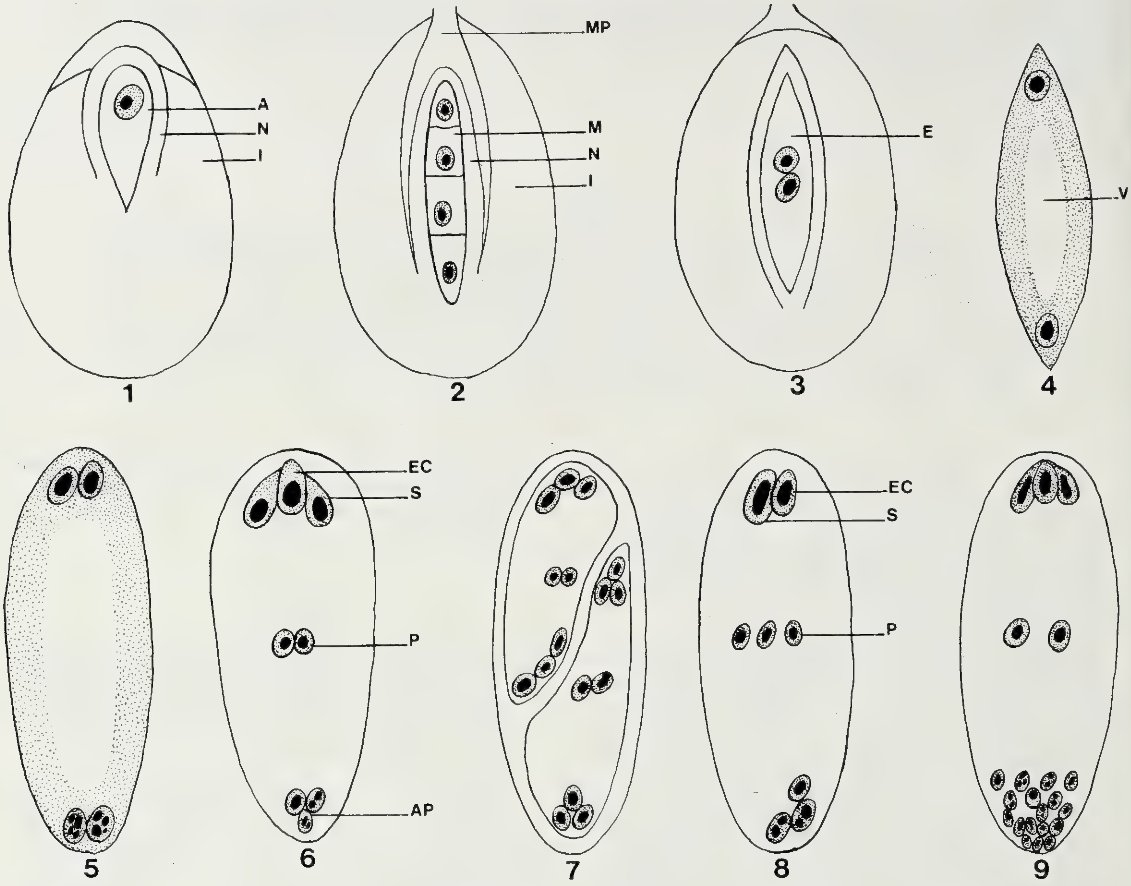

Figs 1–9.—Schematic representation of embryo sac development in *Lantana camara*. 1, archesporium; 2, tetrad; 3 & 4, two-nucleated embryo sac; 5, four-nucleated embryo sac; 6, mature sexual embryo sac; 7, two embryo sacs per locule; 8, three polar nuclei; 8, conglomeration of antipodal nuclei. (A—archesporium; AP—antipodal nuclei; E—embryo sac; EC—egg cell; I—integument; M—megaspore; MP—micropylar region; N—nucellus; P—polar nuclei; S—synergid; V—vacuole.)

DISCUSSION AND CONCLUSIONS

The reproductive studies of Raghaven & Arora (1960) and Khoshoo & Mahal (1967) on *L. camara* have shown that there is a tendency among different open-pollinated cultivars to produce matroclinous progeny when growing together.

Raghavan *et al.* (1960), who studied diploid, triploid and tetraploid cultivars, concluded their study with the observation that reproduction was by obligate apomixis only. Contrary to these findings Khoshoo *et al.* (1967) who studied a wider selection of cultivars, including those of the previous workers, were unable to find a single case of obligate apomixis. Their results ranged from a case of total sexuality in a diploid cultivar to facultative apomixis with 66,7% sexuality or semi-sexuality in a pentaploid plant. In both papers there is speculation about the reproductive mechanisms in *L. camara* but no evidence is led about the mechanisms themselves. It is also clear that the same material gave different results, but it is not clear whether this was due to climatological differences or not.

The tendency to produce matroclinous progeny clearly indicates a high degree of self-fertilization or some kind of asexual reproduction. That emasculated bagged flowers did not produce any seed implies that reproduction was either sexual or apomictic, accompanied by pseudogamy (Khoshoo *et al.*, 1967). Tatachar (1940) has reported the occurrence of double fertilization.

These conflicting indications of apomictic reproduction pointed to the need for the current investigation to determine what mechanism was involved in the reproduction of *L. camara*.

a) *Occurrence of sexual embryo sacs*

54,7% of the ovules investigated by us produced a normal sexual monosporic eight-nucleated embryo sac of the polygonum type (nomenclature according to Maheshwari, 1950) and were found in diploid (2n = 22), triploid (2n = 33) and tetraploid (2n = 44) plants, but not in pentaploids (2n = 55) and hexaploids (2n = 66).

The percentage occurrence of these normal sexual embryo sacs ranged from the extremes of 0% in one plant to 95% in another. Diploid plants produced an average of 69,2% sexual embryo sacs,

TABLE 1.—Embryo sac analysis of 20 cultivars of *Lantana camara* in South Africa. Twenty embryo sacs were counted in each cultivar

Plant no. (Stirton)	Chromosome no.	Number of unpaired chromosomes	Embryo sacs			
			Normal	2 sacs	3 polar nuclei	Many antipodal nuclei
6882	22	—	10	10	—	—
7066	22	—	13	4	2	1
7311	22	4,4	19	0	1	—
7314	22	4,3	17	2	1	—
7361	22	4,1	14	6	—	—
7374	22	—	10	10	—	—
6878	33	3,5	11	9	—	—
6883	33	2,5	17	3	—	—
7348	33	3,2	13	7	—	—
7381	33	2,8	18	—	2	—
7383	33	6	18	2	—	—
7384	33	6,4	13	6	1	—
7387	33	2,8	15	4	1	—
7393	33	3	2	18	—	—
7394	33	5,2	7	13	—	—
7087	44	4,3	5	13	2	—
7230	44	0,9	14	6	—	—
7351	44	0,7	3	17	—	—
5287	55	3,1	—	20	—	—
7058	66	5,4	—	20	—	—
		Average	10,95	8,5	0,5	0,05

ranging between 50% and 95% among plants. Triploids ranged from 10% to 90% with an average of 63,3% sexual embryo sacs. Tetraploids produced an average of 36,7% sexual embryo sacs and showed a range of 15% to 70%.

It is clear from these results that there are large differences within each polyploid group in the percentage of normal sexual embryo sacs produced and as the polyploid level increases, the number of sexual embryo sacs produced drops off rapidly until none are produced in the pentaploid and hexaploid plants. Although we cannot yet furnish any cytogenetic evidence to explain these phenomena, we can conclude that the occurrence of a polygonum type embryo sac proves that *L. camara* has at least the potential to reproduce sexually.

Perhaps the most surprising find of this investigation is the high average percentage (63,3%) of sexual embryo sacs that were found within the triploid series. There are, however, indications that cytogenetic irregularities during the development of the embryo sac occur. These irregularities can be seen in the form of chromosome laggards during anaphases (Fig. 10).

b) *Occurrence of abnormal embryo sacs*

Junell (1934) and Khaleel *et al.* (1972) have described the occurrence of more than one archesporium cell during the early stages of embryo sac development, but we were unable to find any in our material.

It has also been reported in the literature that all four megaspores can undergo development. This has been seen only rarely by Tatachar (1940) in *L. indica* Roxb., but appears to be a frequent occurrence in *L. camara* L. and *L. involucrata* L. (Junell, 1934) and in *L. aculeata* L. (Khaleel *et al.*, 1972). We found a low rate of degeneration of the nonfunctional megaspores. In one ovule two megaspores persisted with a 4-nucleated embryo sac. No evidence for the development of an additional megaspore into an embryo sac could be found.

In all cases where two embryo sacs per locule (42,5%) were found, these embryo sacs were positioned in the polar regions. We did not encounter any cases in which the two embryo sacs were positioned together in the equatorial region. This might mean that both the embryo sacs were sexual and derivatives of two megaspores. However, the polar positions of the two embryo sacs do not totally exclude the possibility of apospory. If apomixis occurs in the form of apospory, this polar position may be accounted for by the constraints of development being such that the space available only allows for a linear development between the poles.

In 2,5% of the embryo sacs examined, a third polar nucleus was encountered. In all such cases the egg apparatus consisted of one synergid and an egg cell. This observation is normal, but the frequency is much higher than one might expect (Maheshwari, 1963). Since these embryo sacs are sexual, their frequency could be added to those of the normal sexual embryo sacs to give a total of 57,25% embryo sacs for that class.

Tatachar (1940) and Padmanabhan (1959) observed an increase in the size of the three antipodal cells even before the egg apparatus was completed. This increase in cell size is accompanied by mitotic divisions resulting in 4–8-nucleated antipodal cells in the mature embryo sacs of *L. camara* and *L. indica.* This phenomenon was not observed by Khaleel *et al.* (1972) in *L. aculeata.* We have

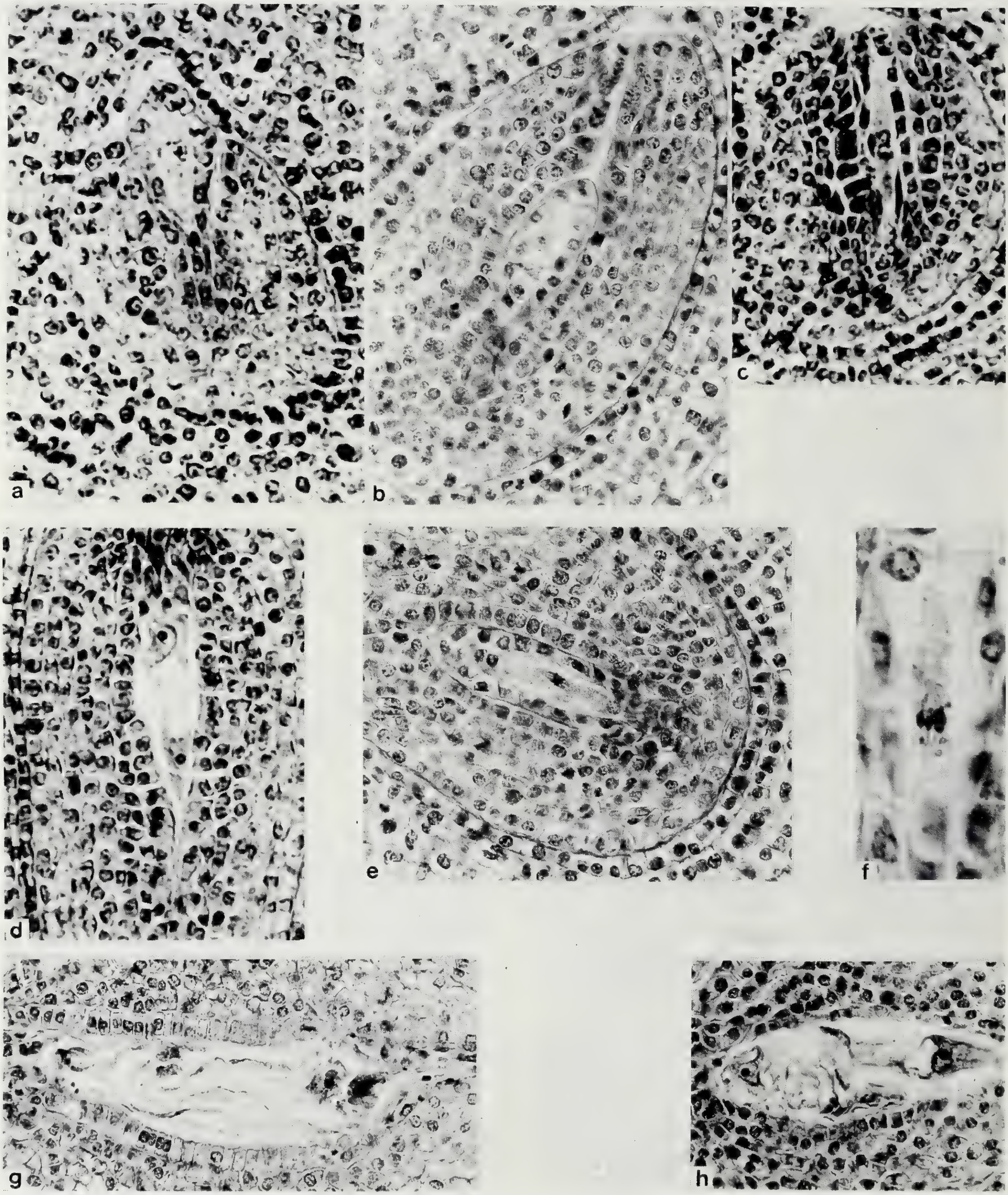

FIG. 10.—Photomicrographs of embryo sac development in *Lantana camara.* a, archesporium; b megaspore; c & d two-nucleated embryo sac; e & f cell division during development of the embryo sac (note fragments of chromosomes not participating in metaphase in f—2n=33); g & h, formation of two embryo sacs per locule, (f ± × 2880; rest ± × 1800.)

encountered a single embryo sac (in *Stirton* 7066, PRE) in which there was a conglomeration of about 20 nuclei, but no separate antipodal cells could be distinguished. So with only one out of 400 ovules studied resembling this phenomenon, we can state that we observed a significant increase neither in cell size nor in the number of nuclei in the antipodal cells of our material.

c) *Seed-setting and microsporogenesis*

Differences in seed-setting by different cultivars of *L. camara* have been reported by Tandon & Bali (1955), Natarajan & Ahuja (1957) and Khoshoo & Mahal (1967). Natarajan *et al.* (1957) did not find any correlation between irregularities in microsporogenesis and seed-setting. Our own data support their findings, as we did not find a correlation (r = -0,0456) between any irregularities in microsporogenesis and the development of abnormal embryo sacs.

In conclusion, it is clear that, although we have shown the occurrence of sexuality in *L. camara* in the form of polygonum type embryo sacs, we have not yet obtained definite evidence for the occurrence of apomixis. The occurrence of two embryo sacs per locule might be attributable to apospory or it might be a result of sexuality where two embryos were formed from two megaspores.

ACKNOWLEDGEMENTS

We are indebited to Dr H. Liebenberg (Department of Genetics, University of Pretoria) for his advice and suggestions and are grateful to Miss A. M. Alberts and Miss Claire Smith (B.R.I., Pretoria) for, respectively, technical assistance and preparation of sketches.

UITTREKSEL

Twintig kiemsakke van elk van twintig verskillende Lantana camara *L. kultivars wat in Suid-Afrika aangepas is, is ondersoek. Die normale geslagtelike kiemsakke was monosporiese agtkernige kiemsakke van die polygonum tipe en het in 55% van die materiaal voorgekom. Verskeie afwykings van hierdie toestand het egter voorgekom. Soms kon een kern nie in 'n sinergiede verander nie en in dié gevalle kom daar drie poolkerne voor.*

In teenstelling met gepubliseerde inligting het die antipodale selle nie vergroot of meerkernig geraak nie. Die bestaan van geslagtelikheid word dus bewys maar geen bepalende bewys vir die voorkoms van apomiksie is gevind nie. Die voorkoms van twee kiemsakke per vrughok mag die resultaat wees van aposporie of geslagtelikheid waar twee kiemsakke uit twee megaspore ontwikkel.

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Stomatal area as an anatomical criterion for the determination of chromosome number in the *Eragrostis curvula* complex

J. J. SPIES*

ABSTRACT

Twenty stomatal areas of each of 55 *Eragrostis curvula* (Schrad.) Nees plants were determined. An increase in polyploid level is shown to be moderately correlated with an increase in stomatal area. However, the extent of overlap in stomatal areas between different polyploid levels is too great to use this character for the determination of the polyploid level above the diploid level. All diploid *E. curvula* plants have an area of less than 280 μ^2, whereas the tetraploid plants have areas greater than 320 μ^2. It is therefore possible to identify diploid *E. curvula* plants on the basis of their stomatal area.

INTRODUCTION

A correlation exists between cell size and the ploidy level of the cell as polyploid cells are usually larger than the cells of their diploid counterparts (Stebbins, 1950; Allard, 1960). This fact has led cytogeneticists to search for suitable cells which could be used to determine chromosome number accurately without a study of the chromosomes. Blakeslee & Avery (1937) used pollen size to distinguish between different polyploid levels in *Datura stramonium*. De Wet (1954) used stomatal length as a criterion for a similar study in the genus *Danthonia*. These studies have not always given the desired results. The most successful results have always been obtained from induced polyploidy where the chromosome number of a single plant has been altered by the use of chemicals such as colchicine (Blakeslee & Avery, 1937; Biswas & Battacharyya, 1976).

The aim of the current investigation was to determine to what extent this method could be used for predicting chromosome numbers in the *Eragrostis curvula* (Schrad.) Nees complex.

MATERIAL AND METHODS

Plants of the *E. curvula* complex were collected in the field throughout South Africa and were transplanted in the Pretoria National Botanical Garden (Vorster, 1978). The chromosome numbers of these cultivated plants were determined by Vorster (1978).

Leaves of 55 of these plants (Table 1) were sampled during March 1981. After 24 hours fixation in F.A.A. fixative, epidermal scrapes of the abaxial epidermis were prepared following the method of Metcalfe (1960) with slight modifications. Safranin and Methylene Blue were used for staining the epidermal scrapes.

Twenty stomata from each plant were measured. Measurements of the stomatal area were made from photomicrographs. A Kontron MOP–AMO2 image analyser was used for determining the stomatal area.

RESULTS AND DISCUSSION

The average stomatal area of each plant is shown in Table 1. These stomatal areas were plotted graphically (Fig. 1). A correlation factor of 0,6774 was found to exist between chromosome number and stomatal area for each plant. This correlation is represented graphically in Fig. 1.

From Table 2 it is clear that the only homogeneous group in this study was the diploid (2n = 20) group. This group showed a standard deviation of 21,79. From Fig. 1 it is evident that the diploid group is the only group with almost no overlap with any other group. The only overlapping that occurred was between the diploid group and one pentaploid plant (*Vorster* 334). During a cytogenetical re-examination that followed this anatomical study, it was found that this plant was indeed a diploid and not a pentaploid. As the Vorster collection was made and transplanted before 1978, the possibility exists that this plant could have reverted to a diploid plant or that the plant was wrongly numbered.

A meiotic analysis of the unpaired chromosomes of *Vorster* 334, showed an average of 5,75 unpaired chromosomes per cell (Vorster, 1978). Unfortunately no embryosac analysis was done on this plant during the present study. It is clear, therefore, that this is a very unstable plant and, although the degree of apomictic reproduction is not known, the chromosome number of this plant could have been altered in various ways. From these results it appears that it can be predicted with a high degree of confidence that any *E. curvula* plant with a stomatal area of less than 280 μ^2 will be diploid.

An unexpected high standard deviation was encountered in the tetraploid (2n=40) group. This results from the fact that the tetraploid sample can be divided into two groups and a big gap of more than 50 μ^2 exists in the area measurements between *Vorster* 422 and *Vorster* 989. The first group corresponds with the regression line drawn in Fig. 1. The second group (*Vorster* 989, 750, 303, 797 and 210) have very large stomatal areas. The average stomatal area (502,37 μ^2) of the second group is almost as large as the average stomatal area (510,41 μ^2) of the octoploid (2n=80) group. It is possible that this might be a case of divergent evolution occurring, or that two different sources exist from which these two different groups have evolved. It

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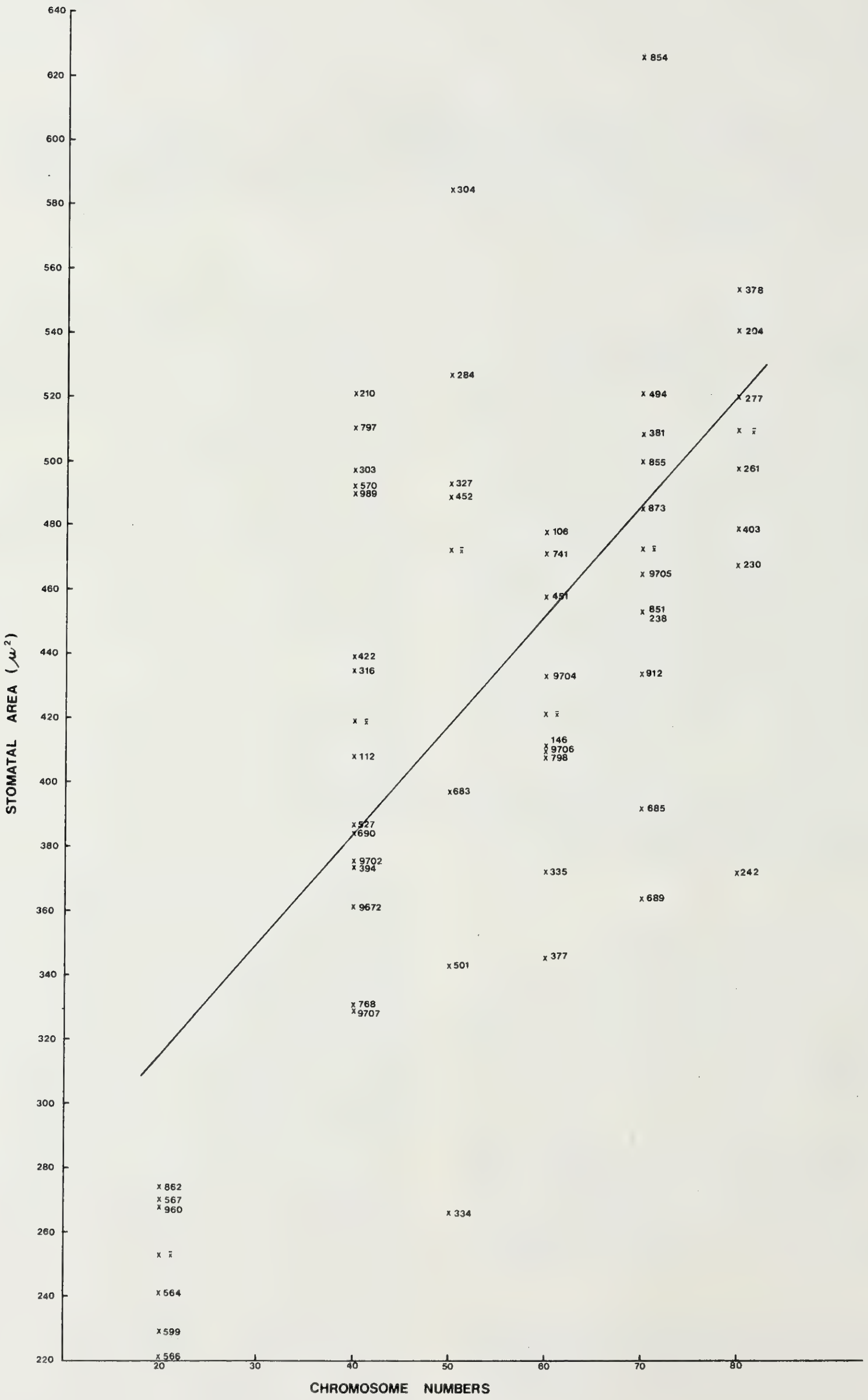

FIG. 1.—Correlation between chromosome numbers and stomatal areas in selected representatives of the *Eragrostis curvula* complex.

TABLE 1.—List of plants used for this study

Locality	Collectors no. (Vorster)	Chromosome no. (2n=)	Stomatal area (μ^2)
2217CA	422	40	439,17
2523BD	564	20	241,64
2524CA	566	20	221,07
2524CA	567	20	270,02
2530BD	683	50	397,41
2530DB	685	70	392,78
2531DD	960	20	268,12
2623BB	559	20	229,61
2625CD	146	60	410,19
2628DD	451	60	458,84
2629CA	452	50	489,76
2630AA	690	40	384,26
2630AB	689	70	364,51
2725BB	106	60	478,98
2728CD	277	80	520,17
2730BB	261	80	498,14
2730DD	204	80	541,82
2823DA	527	40	387,24
2824BD	112	40	408,86
2825BC	501	50	343,49
2826CB	494	70	521,86
2828DA	284	50	526,42
2829CB	238	70	452,31
2829DB	242	80(40)*	372,79
2830DB	210	40	521,1
2924CC	750	40	492,48
2926BB	304	50	585,65
2927AA	303	40	497,35
2929CC	989	40	490,1
2929DA	230	80	468,97
3023DB	768	40	330,64
3025BD	316	40	435,31
3025CB	741	60	471,82
3027AA	327	50	493,11
3027CB	334	50(20)*	266,37
3027DA	335	60	372,94
3028BD	394	40	374,55
3029CD	398	60	408,42
3127AD	381	70	509,54
3128BD	403	80	479,32
3128CA	378	80	554,04
3128CD	377	60	345,66
3224BA	797	40	510,8
3321BD	912	70	434,1
3324BB	862	20	274,34
3324DD	851	70	453,57
3324DD	854	70	627,64
3325CC	855	70	500,82
3418BB	873	70	485,52
Transkei	9702**	40	375,94
,,	9703**	40	329,91
,,	9704**	60	433,36
,,	9705**	70	465,67
,,	9706**	60	410,09
,,	9672**	40	361,97

* These plants were re-examined cytogenetically at a later stage and it was found that *Vorster* 242 had 40 chromosomes and *Vorster* 334 had 20 chromosomes (see text)

** Collected by De Winter

should prove interesting to have a closer look at morphological differences between these two tetraploid groups. It may also be significant to note that all plants in this 'abnormal' group were originally collected in mountainous areas.

A large degree of variation (standard deviation = 87,99) exists in the pentaploid (2n=50) group. Because the pentaploid group tends to be genetically unstable (Vorster, 1978), it will be necessary to undertake a cytogenetical study on this group again, to determine whether chromosome instability is responsible for this excessive variation.

The abnormally large stomatal areas found in some of the tetraploid and pentaploid plants are responsible for the fact that the hexaploid group has a relative lower average stomatal area than both above-mentioned groups. The hexaploid (2n=60) group is relatively homogeneous with regard to the stomatal area (standard deviation = 44,59) and this fact is also reflected in their relative normal meiotic behaviour where an average of 1,64 unpaired chromosomes per cell were found (Vorster, 1978).

With the exception of *Vorster* 854, the heptaploid (2n=70) group shows relatively little variation. This fact corresponds with the observation that heptaploid plants in this study have an average of 4,52 unpaired chromosomes for each meiotic cell (Vorster, 1978). Pentaploid plants showed an average of 5,71 unpaired chromosomes per cell. The heptaploid plants are, therefore, genetically more stable than the tetraploid plants. This fact is clearly reflected in this study by the more limited variation of stomatal areas of the heptaploid plants in comparison with the pentaploid plants.

In the octoploid (2n=80) group only one deviation from the normal acceptable distribution was found. This plant *(Vorster* 242) was studied cytogenetically and found to be tetraploid (2n=40). This might be due to secondary haploidization or a wrong number might have been used somewhere during different collecting and transplanting operations.

CONCLUSIONS

From the results of this study, it is clear that an increase in stomatal area is correlated with an increase in polyploid level (Fig. 2). However, the extent of overlapping of stomatal areas between different polyploid levels of *E. curvula* is too great for the prediction of the polyploid level by this means. The only exception in this regard is the diploid group. All diploid plants had areas of less than 280 μ^2, whereas the other polyploid levels had values above 320 μ^2.

The only published example where cell size has been used directly to determine polyploid level, is with induced polyploidy (Blakeslee & Avery, 1937; Biswas & Battacharyya, 1976). The present results indicate, therefore, that it might be possible to use cell size as a criterion for determining chromosome numbers, but only when working with very closely related plants exhibiting little morphological divergence and originating from similar environments. The De Winter collection included in this study, was sampled from a small area and consists of morphologically almost identical plants but having different chromosome numbers. This group shows a correlation coefficient of 0,953. It might therefore be possible to use this method successfully if the following selection criteria are strictly applied:

1) Collect only morphologically similar plants
2) Collect only in one geographical area

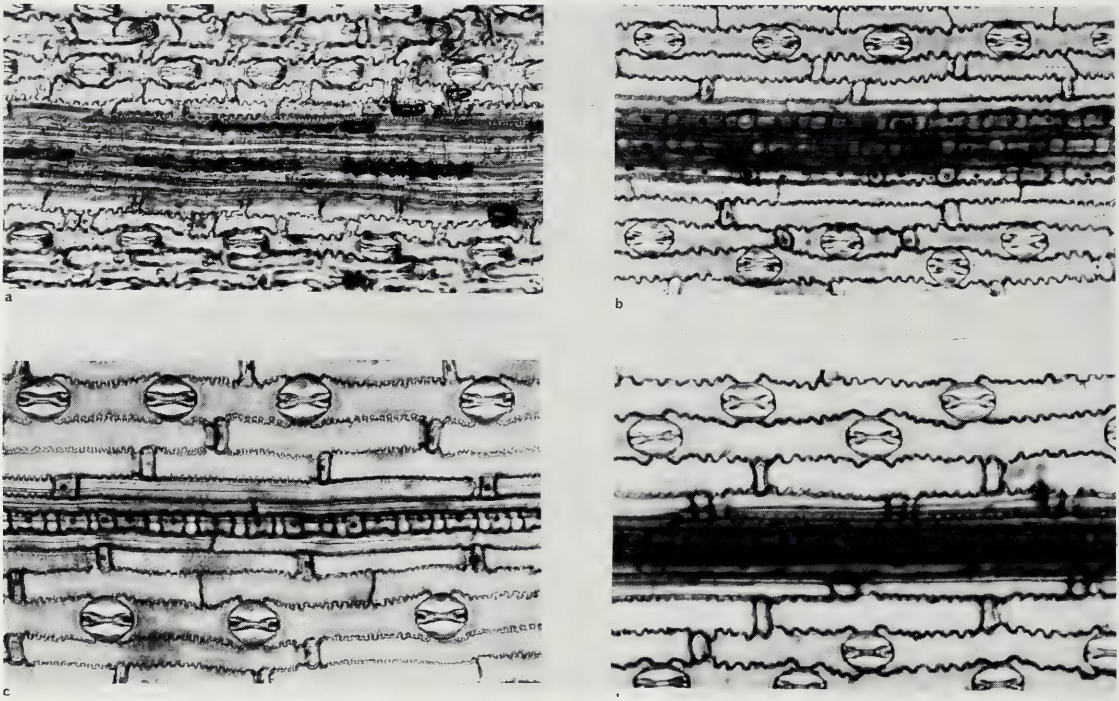

FIG. 2.—Photomicrographs of stomatal areas of *Eragrostis curvula* (×1860) a) 2n=20 b) 2n=40 c) 2n=60 d) 2n=80.

TABLE 2. — Average stomatal area (μ^2) of each plant for the polyploid levels of the *Eragrostis curcula* complex

2 n	20	40	50	60	70	80
Average stomatal area of each plant (micron^2)	221,07	329,91		345,66	364,51	
	229,61	330,64	343,49	372,94	392,78	468,97
	241,64	361,97	397,41	408,42	434,1	479,32
	266,37	372,79				
	268,12	374,55	489,76	410,09	452,31	498,14
	270,02	375,94	493,11	410,19	453,57	520,17
	274,34	384,26	526,42	433,36	465,67	541,82
		387,24	585,65	458,84	485,52	554,04
		408,86		471,82	500,82	
		435,31		478,98	509,54	
		439,17			521,86	
		490,1			627,64	
		492,48				
		497,35				
		510,8				
		521,1				
$\bar{x}$	253,02	419,53	472,64	421,14	473,48	510,41
S.D.	21,79	65,01	87,99	44,59	70,1	34,17

UITTREKSEL

Twintig huidmondjie oppervlaktes per plant van 55 Eragrostis curvula *plante is bestudeer. 'n Verhoging in poliploïede vlak is noemenswaardig gekorreleer met 'n toename in huidmondjie oppervlakte. Die mate van oorvleueling in waardes vir huidmondjie oppervlaktes is egter te groot om hierdie eienskap te gebruik vir die bepaling van die poliploïede vlak bo diploïed vlak. Alle diploïede* E. curvula *plante het 'n oppervlakte van minder as 280* μ^2 *gehad. Dit is dus moontlik om diploïede plante te identifiseer op grond van hulle huidmondjie oppervlaktes.*

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Destruction of the *Phoenix/Hibiscus* and *Barringtonia racemosa* Communities at Richards Bay, Natal, South Africa

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ABSTRACT

The destruction of the *Phoenix/Hibiscus* and *Barringtonia racemosa* Communities described by Venter in 1972 on the southern shores of Richards Bay is reported. The cause was the artificial opening of a new mouth about 5,5 km south of the original mouth, which increased tidal range and salinity. These swamp communities occupied a narrow band about 6 ha in area behind the *Bruguiera gymnorrhiza* Community. An estimated 95% of the communities was affected and only on the landward border were some isolated remnants of species such as *Acrostichum aureum, Hibiscus tiliaceus* and *Phoenix reclinata* detected. Young stands of *Phragmites australis,* seedlings of *Bruguiera gymnorrhiza* and *Avicennia marina* and epipelic algae are recolonizing the affected area.

INTRODUCTION

The construction of Richards Bay Harbour resulted in the Richards Bay Lagoon (28°49' S and 32°05' E) being divided into a harbour zone and a natural sanctuary by the construction of a berm wall and the opening of a new mouth for the nature reserve during 1975. Begg (1978) reports on the many abiotic and biotic changes occurring after the habilition of the harbour. This work focuses on one of these changes affecting vegetation.

Tree mortality along the Zululand Coast has been described previously. Breen & Hill (1969) reported on a mass mortality of mangroves of the Kosi Estuary (Natal) in 1965 following natural closure of the mouth for five months. Bruton & Appleton (1975, in Begg, 1978) described the death of a mangrove swamp at Mgobezeleni Lake (near Sodwana Bay) following the construction of a bridge that impeded tidal flow and caused the swamps to be flooded.

During studies on Natal estuaries (Ward, MS) and on the conservation priorities between Richards Bay and Mlalazi Mouth (Weisser, MS) the vegetation of the southern shores was remapped, sampled with eight relevés and compared with findings of Venter (1972), who studied the vegetation before the harbour development.

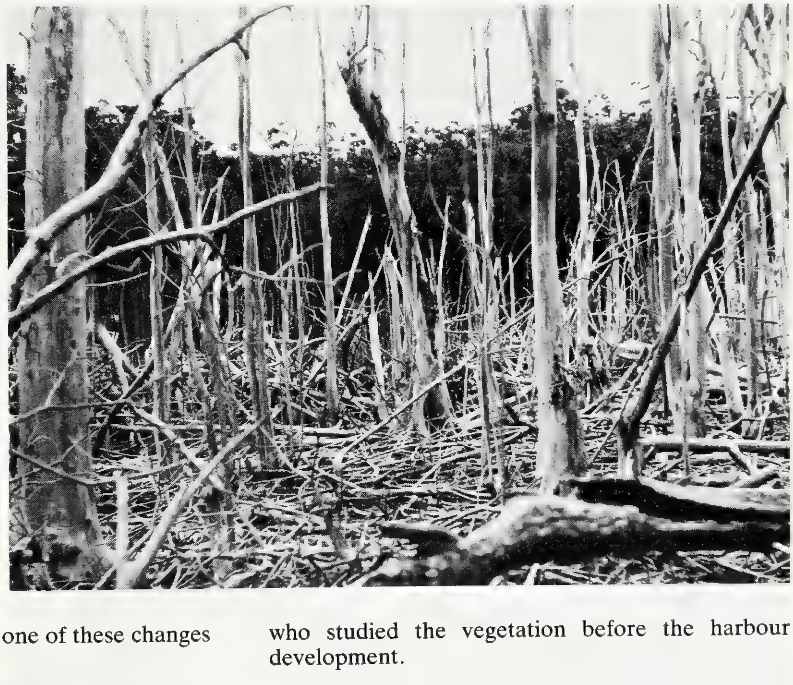

FIG. 1.—Remnants of *Phoenix/Hibiscus* and *Barringtonia racemosa* Communities on southern shore of Richards Bay destroyed by increased tidal range and salinity following opening of new mouth at Richards Bay. In background landward side of *Bruguiera gymnorrhiza* Zone.

RESULTS

During mapping, the almost complete destruction of 6 ha of the *Phoenix/Hibiscus* and *Barringtonia racemosa* Swamp Communities (*sensu* Venter, 1972) in the Richards Bay Sanctuary Area was observed. Dead trees of up to 12 m tall were found and most of the trunks of the bigger trees were still upright (Fig. 1). At high spring tide water completely flooded the dead forest.

The opening of the new mouth in 1975 about 100 m

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TABLE 1.—Eight relevés of the *Bruguiera gymnorrhiza* and *Phoenix/Hibiscus* Communities in the study area. The values correspond to Braun-Blanquet cover-abundance estimates (Braun-Blanquet 1964). The plots 25 m^2, were approximately level, with muddy substrate and usually with stagnant water (dated 1980.11.20–24)

Relevé No.	429	428	427	441	442	443	446	445
Total cover %	80	50	60	10	6	15	70	7
Bruguiera gymnorrhiza	5	4	4	1				1
Avicennia marina			+		r			
Phragmites australis				2	2	2	4	+
Acrostichum aureum							2	1
Phoenix reclinata							1	1
Barringtonia racemosa								+

away from the *Phoenix/Hibiscus* and *Barringtonia racemosa* Communities clearly resulted in the death of these communities. It caused the pre-harbour development tidal range of 0,35 m to increase to 1,63 m in April 1977 (Begg, 1978) and the water salinity to increase, consequently the death of the plants may be attributed to a combination of these two factors. A few, isolated survivors and resprouting plants of *Phoenix reclinata* and *Acrostichum aureum* were found to occur near the southern corner of the bay, on slightly higher parts farthest from the sea (Table 1, relevé 445). A plant that has lately increased in the affected area is *Phragmites australis* which, in places, forms dense stands between the dead trunks and debris (Fig. 2 and Table 1, Relevés 441, 442, 443, 446). *Bruguiera gymnorrhiza* seedlings and *Avicennia marina* saplings were observed to be colonizing the area (Table 1, Relevés 441 & 445). This suggests a landward extension of the Mangrove Community. Open parts of the destroyed zone were colonized by epipelic (= growing on mud) algae.

Venter (1972) described the *Phoenix/Hibiscus* Community prior to its destruction as occupying a small zone immediately behind the *Bruguiera gymnorrhiza* Community at the south-eastern shore of Richards Bay. Landward it bordered on the *Barringtonia racemosa* Community (see Fig. 3 in Venter 1972) and on primary or secondary Dune Forests. It was a dense thicket formed mainly by the palm *Phoenix reclinata, Hibiscus tiliaceus* and the fern *Acrostichum aureum.* Other species present were *Rapanea melanophloeos, Ficus trichopoda, F. capensis, Syzygium cordatum, Bruguiera gymnorrhiza* and *Avicennia marina.* The last two species were in poor condition and were probably remains of the neighbouring *Bruguiera gymnorrhiza* Community which, in the course of time, was apparently displaced by the *Phoenix/Hibiscus* Community.

Climbers were *Mikania cordata, Ipomoea cairica, I. congesta, Dioscorea sylvatica* and *Rhus nebulosa,* the first two species being particularly common. Field layer species recorded were *Acrostichum aureum, Nidorella auriculata, Phragmites australis, Typha latifolia* subsp. *capensis, Cyperus alternifolius, Scadoxus magnificus* and *Blumea lacera.*

Many *Phoenix reclinata* trees were cut by Zulu people living nearby to tap the sugar-rich sap. The damaged plants coppice freely from the base to form dense thickets.

The *Barringtonia racemosa* Community was quantitatively studied by Venter (1972), who took samples at three places nearby: at Mzingazi Lake, west

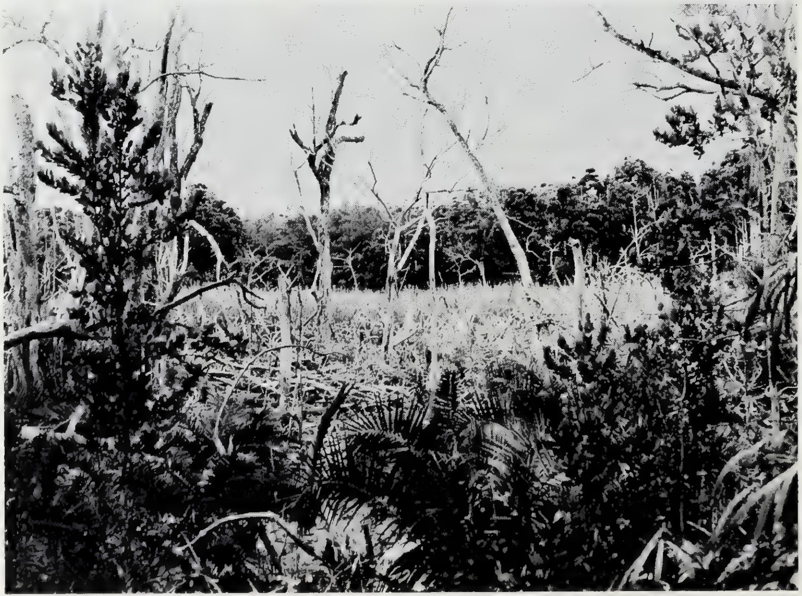

FIG. 2.—View across part of destroyed zone. In this area *Phragmites australis* and *Bruguiera gymnorrhiza* adapted well to changed conditions and are now increasing.

of Richards Bay town, and on the southern shores of Richards Bay. He found a community of high density in the canopy layer (1 245 plants ha^{-1}) which had a basal cover of 131,2 m^2 ha^{-1}. The habitat was muddy and covered with water. *Barringtonia racemosa* was predominant with an importance value of 57,5, followed by *Syzygium cordatum* with 12,6. Other common canopy species were *Voacanga thouarsii, Bridelia micrantha* and *Macaranga capensis.* In the understorey, *B. racemosa* was also dominant with other species being *Tarenna pavettoides* and *Schefflera umbellifera.* The density was 975 plants/ha. Climbers were common, especially the ferns *Stenochlaena tenuifolia* and *Phymatodes scolopendria* with *Smilax kraussiana* and *Canthium gueinzii.* The field layer was dominated by seedlings of *Barringtonia racemosa.* Other species present were *Canthium gueinzii* and *Scleria angusta.* Epiphytes were scarce. Only *Microsorium punctatum, Cyrtorchis arcuata* and *Ficus craterostoma* (hemi-epiphyte) occurred.

It was not possible to establish to what degree this description truly represents the vegetation of the area destroyed, as some samples for Venter's analysis were taken outside the study area (e.g. Mzingazi Lake). However, *Voacanga thouarsii* and *Rauvolfia caffra* would seem to have played a more dominant rôle in the study area. *Nephrolepis biserrata* was observed as an epiphyte low down on stems of dead trees.

The death of the *Phoenix/Hibiscus* and *Barringtonia racemosa* Communities in the Richards Bay Sanctuary owing to the opening of the new mouth was an unforeseen penalty that was paid for the opening up of the Richards Bay Harbour and is an example of how infra-structural developments may affect even areas that were specifically set aside as natural sanctuaries.

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UITTREKSEL

Verslag word gelewer oor die verwoesting van Phoenix/Hibiscus *en* Barringtonia racemosa *gemeenskappe (ongeveer 6 ha) aan die suidkus van Richardsbaai. Dit is veroorsaak deur die skepping van 'n kunsmatige uitloop ongeveer 4 km suid van die oorspronklike monding. Die getygrense en die soutgehalte van die water is hierdeur verhoog. Hierdie moerasgemeenskappe het 'n smal strook agter die* Bruguiera gymnorrhiza *gemeenskap in beslag geneem. Ongeveer 95% van die gemeenskappe is beïnvloed. Geïsoleerde oorblyfsels van spesies soos byvoorbeeld* Acrostichum aureum, Hibiscus tiliaceus *en* Phoenix reclinata *is in die gedeelte van die strook naaste aan die land gevind. Die geaffekteerde gebied word nou ingeneem deur jong groepe* Phragmites australis *asook deur* Bruguiera gymnorrhiza *en* Avicennia marina *saailinge en epipeliese alge.*

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Dune advancement 1937–1977 at the Mlalazi Nature Reserve, Mtunzini, Natal, South Africa, and a preliminary vegetation-succession chronology

P. J. WEISSER*, I. F. GARLAND** and B. K. DREWS*

ABSTRACT

Foredune advancement on a 2 km coastline north of the Siaya Lagoon Mouth was studied using air photos. Between 1937 and 1977 the dunes advanced about 95 m (2,4 m per year). Vegetation was dated according to its position on a profile. If a 2,4 m per year seaward advancement of the dunes is assumed, the following succession chronology is obtained: *Scaevola thunbergii* Foredunes from 0 to 30 years; *Passerina rigida* Open Dune Scrub 30 to 60 years; Closed Dune Scrub 60 to 90 years and Dune Forest beginning at about 90 years. Variation in dune advancement rates on different coastal stretches and for different time intervals was observed and will be reported on later. This dune succession chronology should, therefore, only be seen as a first rough approximation.

INTRODUCTION

Huntley (1977), referring to vegetation mapping in South Africa, indicated that little effort had been expended in monitoring the rates and kinds of change taking place in vegetation. The availability of air photos (dating from 1937 to 1979) of Mtunzini, Natal, afforded the author the opportunity to contribute information in this neglected field. Objectives of this study were to evaluate the adequacy of air photos in monitoring dune advancement and vegetation changes; to measure foredune advancement and calculate advancement rates; and to infer a dune-succession chronology by dating the communities according to their position in a profile.

The two km coastline studied is part of the Mlalazi Nature Reserve and stretches from the Siaya Lagoon Mouth (latitude 28° 58' South, longitude 30° 45' 45" East) north-eastwards. The coast between Mlalazi Lagoon and the Tugela Mouth is one of the few coastlines in Natal where active sand deposition and foredune advancement is occurring. The dunefield there is formed by a series of about 16 phytogenic ridges parallel to the coast and is about 400 m broad. Edwards (1967) and Moll (1972) described dune communities of this region.

METHODS AND METHODOLOGICAL CONSIDERATIONS

The dune vegetation and its advancement were studied by direct inspection of air photos. The information was transferred onto a 1: 10 000 base map using a Bausch & Lomb ZT-4 Zoom Transfer Scope (=ZTS). This instrument was also employed to draw the base map from the orthophoto map 2831 DD 21 'Mtunzini' (1977). Interpretation of aerial photographs was aided by a Topcon Stereoscope. Roads were mainly used as matching lines. Limits of the foredunes were drawn onto overlays and their progression was measured with a 1/10 mm graduated ocular. About one hundred systematic sampling lines were drawn perpendicular to the coast on the base map starting at the Siaya Lagoon Mouth and going northwards. A north-eastward longshore advancement of the Siaya Lagoon Mouth of about 740 m from 1937 to 1977 was found, i.e. about 17,4 m per annum. Air photos 54693 (Job 117, of 1937.05.05), 6447 (Job 400, 1957.05.24), 5665 (Job 608, 1969.08.18) and the orthophoto 2831 DD 21 (Job 498/91, June 1979) were used. Ground truth was gathered on 1974.09.15, 1975.11.03, 1978.06.29, 1980.03.27, 1980.05.15, 1980.06.11 and 1980.06.12.

The potential and limitations of air photos in vegetation studies have been discussed by Edwards (1972) and, in relation to dune vegetation in Zululand, by Weisser (1979). Concerning this study the following points should be borne in mind. The photographs are at different scales, and were not taken at the same time of the year which impairs their comparability. Another factor is the differing resolution of the air photos, the 1937 photos being the weakest.

The evaluation of the results is complicated because dune advancement is not a linear process. It occurs in pulses, each pulse corresponding to the detection of an additional dune ridge on the air photo. There is a time lag between the establishment of *Scaevola thunbergii* seedlings, the accumulation of sand and the appearance of the new ridge on the air photo. These dunes are at first isolated and later colaesce to a coastal parallel ridge (Figs 1 & 2).

The distance between the dune ridges is not uniform. At Twinstreams, south of the Siaya Mouth, the average distance between the last four dune crests was 25 m. Distances measured on the transect published by Moll (1972) over the whole dune field suggest a distance of about 22 m between crests.

RESULTS AND DISCUSSION

Air photos of a scale equal to or less than 1: 30 000 were found adequate for monitoring and measuring the advancement of the foredunes provided matching lines or points were available. Air photos of 1977 and 1979 were discarded, because the small area covered provided insufficient matching points in the optical field of the ZTS.

Fig. 3 summarizes the distance measurements as interpreted from the photos. From 1937 to 1957 (20 years), the *Scaevola thunbergii* Foredunes advanced

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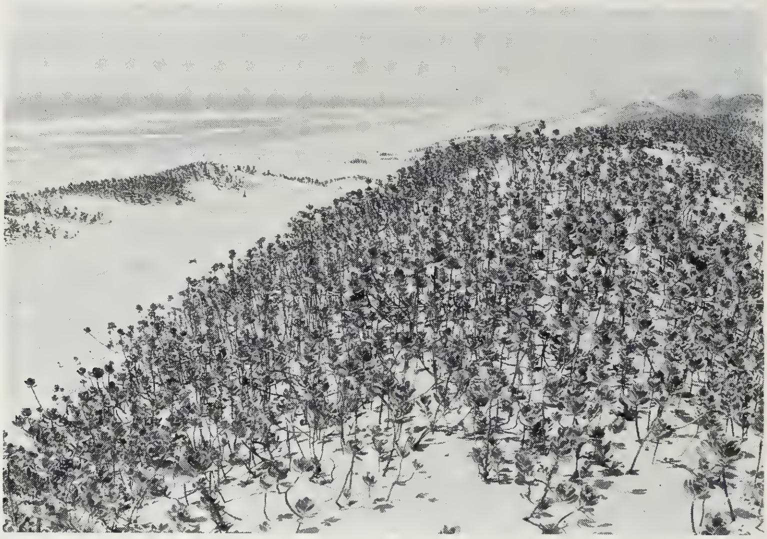

FIG. 1.—Foredunes at Twinstreams, Mtunzini (Nov. 1975). New *Scaevola thunbergii* dune being formed. First dune started in June 1973 (observation by I. Garland).

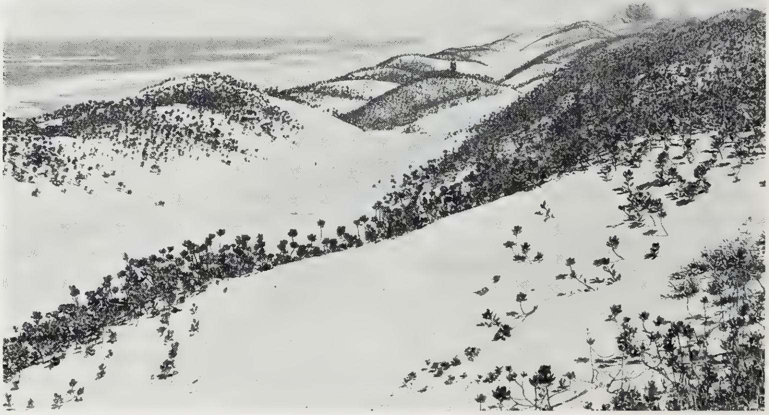

FIG. 2.—Picture taken from approximately same point as in Fig. 1. It shows how sand accumulation has progressed from November 1975 to June 1978. At this time, seedlings of *Scaevola thunbergii* were already colonizing the beach and starting a new dune ridge.

seawards by about 42 m, in 1969 (after 32 years) the distance had increased to 81 m and in 1977 (after 40 years) to 95,2 m. The average rate of advancement from 1937 to 1977 was 2,4 m per year. No advancement values could be obtained for other plant communities because their limits on the air photos are difficult to interpret consistently. While the seaward limit of the foredunes is well defined and corresponds to a *'limes convergens'* the others are of the *'limes divergens'* type (Van Leeuwen, 1966).

Space/time relations

The distance of dune ridges from the seashore is directly proportional to their age and *vice versa.* The foredune advancement rate of the last 40 years was 2,4 m per year north of the Siaya Mouth. Therefore, it is possible to date the ridges and their vegetation by measuring the distance from the beach.

This possibility of dating vegetation led us to extend our studies south to the farm Twinstreams. Whereas processes and dune advancement values similar to those north of the Siaya Mouth were encountered, the lack of matching points in the limited optical field of the ZTS made precise distance measurements difficult.

On a speculative level, and if the yearly advancement rate of 2,4 m is applied to the transect published by Moll (1972), the positions of the communities on the transect suggest the following succession schedule (Table 1):

(1) It agrees with Moll (1972) in that it takes about 10 years for a dune ridge to be formed under present conditions (Fig. 2).

(2) It will take about 30 years to become invaded and later replaced by the *Passerina rigida* Open Dune Scrub (Fig. 4).

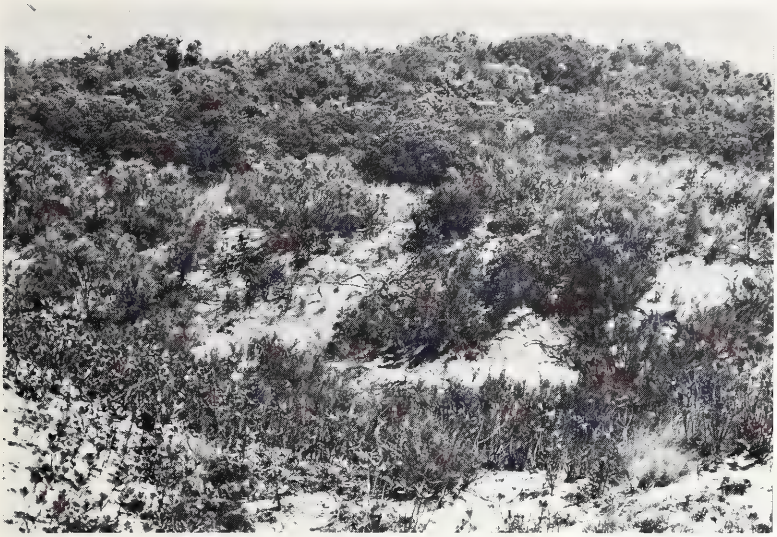

FIG. 3.—In foreground, *Scaevola thunbergii* Community being invaded, and thereby phased out, by grass *Stipagrostis zeyheri* and shrubs such as *Passerina rigida, Colpoon compressum, Canthium obovatum, Apodytes dimidiata, Mimusops caffra* and *Brachylaena discolor.* Closed Dune Scrub lies at top of ridge, concealing Dune Forest (1978.07.29).

(3) It will take about another 30 years before this scrub is replaced by Closed Dune Scrub (Fig. 4).

(4) If protection against seawinds and saltspray is given by the seaward ridges and their vegetation, a Dune Forest could develop after about 90 years, beginning in the dune slacks and later spreading from there.

The reliability of the space/time relation is reduced by the variation in dune advancement rates on different coastal stretches and at different time intervals. In some places, e.g. in the northern part of the Mlalazi Reserve, there has lately been a tendency for the height of the existing dunes to increase instead of new ridge formation and dune advancement seawards taking place. The key factor to the differing deposition of sand, i.e. either in the formation of new ridges or in increasing the height of existing ones, is the establishment of *Scaevola thunbergii* seedlings on the beach and the accumulation of sand around these obstacles. If beach conditions do not allow establishment of *Scaevola thunbergii,* the landward-blown sand will tend to get trapped in the existing foredunes and contribute to their height increase. High and low ridges in Moll's profile suggest that they have held their position adjacent to the beach for varying periods of time before being replaced and outcompeted for sand by new ridges. High dune ridges suggest longer periods near the seafront, during which sand had time to accumulate. The occasional destruction of ridges by unusual storms and tides must also be considered.

A recent increase in the rate of sand deposition is likely, because of the increased sediment load of the Tugela River following agricultural malpractices in the catchment areas. Part of the sand is transported northwards by longshore drift (Orme in Begg, 1978). However, the LANDSAT satellite image No. 1190–07143 of 29th January 1973, shows the sediment plume of the Tugela extending mainly southwards.

The space/time relationships obtained here must be regarded as a first approximation and should be followed up by studies with permanent plots. C. J. Ward (pers. comm.) and MacDonald and Pammenter (MS) have laid out permanent vegetation plots and transects in the Twinstreams area and Mlalazi Nature Reserve which will allow future refinement of this interim dune vegetation-succession chronology.

TABLE 1.—Position and spatial range of dune vegetation and its inferred age assuming a seaward advancement of 2,4 m per year

	Distance of beginning of sere from first pioneer plants (Moll's transect) m	Time taken for succession of community to commence years	Range of community m	Approximate duration of sere (assumed rate of vegetation advance 2,4 m per year) years
Pioneers	0		72	± 30
Passerina rigida Open Dune Scrub	72	30	74	± 31
Closed Dune Scrub	146	60	68	± 28
Dune Forest	214	89		

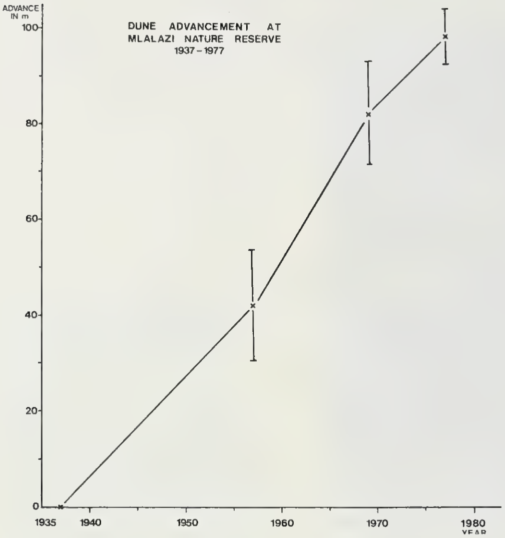

FIG. 4.—Foredune advancement at the Mlalazi Nature Reserve. Total distance of the dune advance 1937–1977 was 95 m and the average rate 2,4 m per year.

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UITTREKSEL

Die voortgang van die voorste duine is bestudeer op 'n 2 km kuslyn noord van die Siaya strandmeermonding deur middel van lugfoto-interpretasie. Tussen 1937 en 1977 het die duine 'n afstand van ongeveer 95 m aangeskuif (2,4 m per jaar). Die plantegroei se posisie is ooreenkomstig hul posisie op die profiel gedateer. Indien aanvaar word dat die seewaartse voortskuiwing van die duine 2,4 m per jaar is, word die volgende chronologiese suksessie verkry: die voorste duine met Scaevola thunbergii *vanaf 0 tot 30 jaar;* Passerina rigida *Oopduinstruikgewas 30 tot 60 jaar; Geslote-duinstruikgewas 60 tot 90 jaar en Duinwoud begin ongeveer by 90 jaar. Verandering in die tempo van duinvooruitgang by verskillende kusstreke, sowel as teen verskillende tydintervalle, is waargeneem. Hierdie chronologiese suksessie van die sandduine moet gevolglik slegs as 'n eerste rowwe skatting gesien word.*

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Aboveground biomass categories of woody plants in a *Burkea africana* – *Ochna pulchra* Savanna*

M. C. RUTHERFORD**

ABSTRACT

Aboveground peak season biomass is given for 11 woody species in each of five belt transects on the Nylsvley savanna study site. Mean aerial biomass for all species was 16 273 kg ha^{-1}, made up of 14 937 kg ha^{-1} wood, 236 kg ha^{-1} current season's twigs and 1 100 kg ha^{-1} leaves with an additional 1 859 kg ha^{-1} of dead wood attached to the individuals. Species which contributed most to total biomass were *Burkea africana* (8 687 kg ha^{-1}), *Ochna pulchra* (2 136 kg ha^{-1}) and *Terminalia sericea* (1 734 kg ha^{-1}). *Grewia flavescens* differed from all other species in having a proportionately larger mass of dead wood and current season's twig biomass. Shrub-sized individuals constituted 11,5% of mean total biomass and 29,7% of mean leaf mass for all species together. Values recorded in the five belt transects differed considerably, for example, leaf area index (LAI) ranged from 0,5715 in belt transect C to 1,0094 in belt transect A. The mean biomass data for the Nylsvley savanna site correspond with available biomass data for savanna vegetation elsewhere in southern Africa.

INTRODUCTION

The South African Savanna Ecosystem Project is being conducted on a portion of the Nylsvley Nature Reserve (3 120 ha in extent), 10 km south of Naboomspruit in the northern Transvaal. The basic ecological characteristics of the study area are described in Huntley & Morris (1978), while the projects overall objectives and research programme are outlined in Huntley (1978).

The study area lies on the edge of the Springbok flats on a slightly raised plateau at about 1 100 m above sea level. Most of the Waterberg System sandstone bedrock is covered by sandy soils belonging mainly to the Hutton and Clovelly forms (Harmse, 1977). Mean annual rainfall is about 630 mm and occurs mainly in summer. The mean annual air temperature is 18,6°C. The study site's past management has included light summer grazing by cattle with small populations of impala and fluctuating populations of kudu present. Fire has occurred irregularly at approximately five year intervals though there is evidence of more frequent fire in the south-western part (belt transects D, E) of the study area. The main vegetation type of the study area has been classified as *Eragrostis pallens – Burkea africana* Tree Savanna (Coetzee *et al.*, 1976) with the most extensive variation of this being the *Eragrostis pallens – Dombeya rotundifolia* variation with dominant trees *Burkea africana* and *Terminalia sericea* and dominant shrubs *Ochna pulchra* and *Grewia flavescens* (Fig. 1). Huntley (1977) suggests that the broad-leaved savanna of the study area is related to the mesic and moist broad-leaved savanna biome of Africa.

Scattered at several localities within the study area are small abandoned native settlement areas which now support a flora very different to that of the remainder of the study area.

The first objective of the Savanna Ecosystem Project has been to determine 'the structure and dynamics of the ecosystem as a whole' (Anon, 1975), and Phase I in the project includes 'the description and quantification of structural features of the ecosystem' (Huntley, 1978). The objectives of the study described in this paper fell within this first phase of the overall ecosystem project, and were to determine the biomass of the main aboveground categories of the woody species present and the variation from one part of the study area to another. This paper is largely limited to presentation of data and detailed discussion of methods is available elsewhere (Rutherford, 1979).

DEFINITION OF TERMS

Biomass is defined as oven dry mass of live, actively or structurally functional organic material and does not include the dead wood category. The categories which were determined included:

- Total biomass, the total living or functional mass.
- Biomass of the stem, mainly wood.
- Biomass of branches, mainly wood. Where stem and branch biomass were not separated, this is referred to as wood biomass.
- Biomass of current season's twigs.
- Biomass of leaves. Current season's twig mass together with leaf mass, that is the total mass of current terminal growth, is referred to as shoot biomass.
- Mass of dead wood (branches and twigs) still attached to the plant individual.
- Leaf area.

All shrubs and trees with stem diameters equal to or greater than one centimetre at 20 cm above ground level were included in the study. Individuals with stems less than one centimetre in diameter were clipped and included in an independent study of

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FIG. 1.—View of the vegetation in a part of Transect A in which aboveground woody plant dry mass (functional and dead) was estimated at 21 602 kg ha^{-1}.

herbaceous layer production. In terms of mass, in both the 1975/76 and 1976/77 seasons, flowering and fruiting was negligible compared to any of the other mass categories and was also very sporadic. Biomass of generative material is therefore not included.

Shrubs were defined as individuals with height less or equal to 2,5 m and trees were taller than 2,5 m. The use of 2,5 m height as a basis for separation of shrub- and tree-sized individuals is arbitrary but 2,5 m is a height above which virtually no browsing by larger herbivores present can take place. It is also a height below which shoot growth points are most commonly damaged after fire on the Nylsvley site.

METHODS

Survey areas

Lubke *et al.* (1976) have described how five belt transects were selected to best represent the woody vegetation of the ecosystem study site. These areas represent the three variations and the subvariations of *Eragrostis pallens — Burkea africana* Savanna of Coetzee *et al.* (1976). These selected areas do not include *Acacia* patches of old abandoned settlements, sandstone hills or occasional rocky outcrops, or fire-break areas. These five areas were used by Lubke *et al.* (1976) for an intensive survey of woody species structure including detection of pattern of distribution. The five areas are designated A in the north-east of the study area through to E in the south-west of the study area.

In the present study, all or part of each of these belt transects was used as basis for estimation of biomass of woody species, respective sample sizes being 0,875 ha in transect A, 1, 6 ha in transect B, 0,8 ha in transect C, 0,96 ha in transect D and 0,96 ha in transect E. The total area sampled for application of biomass relations was therefore 5,195 ha. Belt transects D and E have been set aside for destructive sampling with areas A, B and C being protected. Our own measurements of dimension were used for trees but data of Lubke *et al.* (1976) (using smaller parts of each sample strip) were used for shrub-sized individuals (except for *Grewia flavescens*).

Biomass estimation

The method used involved a destructive phase in which a number of individuals of each of the more important woody plant species were measured for various dimensions (see Appendix 1), then felled and the above defined parts of the plant weighed oven dry. All plant material was dried to constant mass at 85°C. A relational stage followed where dimensions were appropriately related to the various mass categories of the plant resulting in a predictive relation for each species (function types in Appendix 1). A third phase involved a large-scale field survey in which all individuals were measured for the predictor variables in plots of known size, whereupon the predictive relations were applied to give the mass of the various categories per unit ground area.

Because the number of different species involved was too large for equally intensive treatment of each, species were divided into convenient groups, based on plant abundance data available from early surveys.

The first group contained the four species, *Burkea africana, Ochna pulchra, Terminalia sericea* and *Strychnos pungens* in each of which a full size range of up to 49 individuals were processed in detail, providing from primary data, the predictive equations listed in Appendix 1. Leaf area data were obtained from leaf mass data by determination of Specific Leaf Area (cm^2/g) in each species. Stem wood was calculated by subtraction of all other biomass categories from total biomass.

The second group contained the next three, much less abundant species, *Vitex rehmannii, Combretum zeyheri* and *Dombeya rotundifolia*. The method was as in the first group except that the size of the field sample was much reduced, as little as three very carefully selected representative individuals being analysed in full. These restricted data were then plotted out together with relations for the species of the first group and used to determine what constants (if any) should be applied to the equations for the species of the first group to form new predictive equations. This method resulted in quantitative approximations of the biomass categories.

A third group comprised several distinctly rarer species. *Strychnos cocculoides* and *Combretum molle* were subjectively matched according to affinity at the generic level. Two *Securidaca longipedunculata* individuals were sampled in the field since matching here was less obvious. The two *Combretum* species *(C. zeyheri* and *C. molle),* from inspection of several individuals, appeared similar for each biomass category. *Strychnos cocculoides* appeared similar to *S. pungens* except in respect of the relations for total biomass and mass of dead wood.

A fourth group included all other rarer species for which no field mass data existed and there was no clear basis for matching with any particular other species. Here the combined relations of the group with the most reliable data (the first) were used. The above relations are valid for the peak of growth season (based on completion of terminal growth). Almost all field work was done in the 1975/76 season.

A fifth 'group' contained only the multi-stemmed shrub *Grewia flavescens.* The method described above for individual stems was found impractical to apply owing to the prohibitively large numbers of such stems in the enumeration-type survey. The alternative use of a 'whole individual' predictor for dimensions such as that of canopy diameter were found unsuitable owing to large variation in density and spacing of individual stems. Another test showed large scale harvest of all *G. flavescens* individuals over large areas, without recourse to predictive relations, was unacceptable due to several sampling problems. A further approach, which was finally accepted, made use of *G. flavescens* individuals stratified upon four modes of growth and die-back. Mean mass ratios were then applied to each of these different forms for shrub-sized and tree-sized individuals.

RESULTS

Biomass of different plant parts for tree- and shrub-sized individuals of each species is given in Table 1. Biomass proportions are summarized in Table 2. Shrubs had a far greater proportion of terminal growth than trees. It is particularly in current twig biomass of shrubs that exclusion of *Grewia flavescens* greatly reduced the relative contribution of this category. The other biomass categories are little affected by inclusion or exclusion of *G. flavescens.* However, in the dead wood mass category, it is important to differentiate between relative contributions with or without *G. flavescens.* It is particularly the shrub-sized individuals where the exclusion of *G. flavescens* causes a very large decrease in the relative contribution of dead wood mass. That *G. flavescens* differs from other species in respect of relative amounts of twig biomass and dead wood mass may not be merely fortuitous. These two aspects are likely to be linked since the large scale die-off of older parts allows for new self-supported shoot growth only from ground level. There are indications that proportions of dead wood mass in *G. flavescens* can vary greatly with season.

An example of a typical breakdown of biomass categories in a tree species is provided by *Burkea africana* (Table 3). For those species in which stem wood biomass and branch wood biomass were measured separately, that is in *B. africana, Ochna pulchra* and *Terminalia sericea* which make up more than three-quarters of the total biomass of all species, virtually twice as much stem wood as branch wood biomass was found, varying from 2,14 times more in *Burkea africana* to 1,37 times in *Ochna pulchra.*

Four species (Fig. 2) accounted for 81,9% of shoot mass or terminal production. A major contribution of 93,8% to dead wood mass was made by the same four species. Although *Burkea africana* comprised more than half the total biomass, its productivity (terminal) was only about one-third of the total. Conversely, the percentage contribution of *Ochna pulchra* to total terminal production is about twice that of its percentage contribution to total biomass while *Grewia flavescens* productivity rank position of 4 drops to 10 relative to total biomass.

Dead wood was also the only mass category where only three species accounted for more than 90% of the total amount. The mass of dead wood as a percentage of total mass was 79,3% for *G. flavescens,* 10,5% for *Terminalia sericea* and 5,6% for *Burkea africana.* The other separately considered species varied between 1,6 and 4,9%. Three of the four species with the greatest terminal growth capacity also had the highest percentage of dead wood mass. Leaf mass and leaf area differences between species followed the pattern of differences in shoot mass (Fig. 2), with the clear exception of *Grewia flavescens.*

Biomass and leaf area variation within the study site is summarized in Table 4. There were relatively large differences in woody species leaf area index (LAI) from one transect to another (Fig. 3) where, for example, LAI in transect A was 177% of that in transect C.

DISCUSSION

The mean woody species basal (at 20 cm above ground) area (excepting *Grewia flavescens*) is 6,26 m^2 ha^{-1} varying from 7,40 m^2 ha^{-1} in transect A to 4,52 m^2 ha^{-1} in transect C. This basal area is lower than the 8 m^2 ha^{-1} quoted for a long protected savanna woodland with *Burkea africana* dominant in north-eastern South West Africa/Namibia (Rutherford, 1978) and the 8,5 m^2 ha^{-1}, in a *B. africana* dominated community about 7 km from the Nylsvley study area, that had been protected from fire for several decades (Rutherford & Kelly, 1978). The Nylsvley study area has a lower woody species basal area than similar communities elsewhere possibly owing to the more frequent occurrence of fire on the Nylsvley site. This lower basal area is also reflected in a lower total biomass.

The mean total biomass for the Nylsvley site (16 273 kg ha^{-1}) is considerably less than the 22 300

TABLE 1.—Mean mass and leaf area data for the Nylsvley study site*

Species	Size Class	Biomass kg ha^{-1}					Dead Wood Mass kg ha^{-1}	Leaf Area m^2 ha^{-1}
		Total	Stem Wood	Branch Wood	Current twig	Leaf		
Burkea africana	Tree	8 495	5 560	2 512	59	364	462	2 597
	Shrub	193	47	102	8	36	57	257
	Total	8 687	5 607	2 614	66	400	519	2 854
Ochna pulchra	Tree	887	597	210	7	73	23	532
	Shrub	1 250	450	554	30	216	19	1 733
	Total	2 136	1 047	764	36	289	42	2 266
Terminalia sericea	Tree	1 631	1 007	470	9	145	195	889
	Shrub	104	35	53	1	15	9	88
	Total	1 734	1 042	522	10	160	204	977
Grewia flavescens	Tree	91	53		27	11	373	76
	Shrub	164	69		59	36	604	250
	Total	256	123		86	47	977	325
Vitex rehmannii	Tree	742	659		12	71	12	509
	Shrub	74	61		2	11	1	76
	Total	815	719		14	82	13	587
Combretum zeyheri	Tree	691	646		9	36	28	261
	Shrub	0	0		0	0	0	2
	Total	691	646		9	36	28	263
Dombeya rotundifolia	Tree	378	350		7	21	11	145
	Shrub	1	1		0	0	0	3
	Total	380	352		7	21	11	148
Combretum molle	Tree	351	334		3	14	12	104
	Shrub	2	1		0	1	0	4
	Total	353	334		4	15	12	107
Strychnos pungens	Tree	273	265		0	8	8	43
	Shrub	38	33		0	5	1	33
	Total	312	298		0	14	9	76
Strychnos cocculoides	Tree	446	433		1	12	23	57
	Shrub	2	2		0	0	0	2
	Total	448	435		1	12	23	59
Securidaca longipedunculata	Tree	205	199		1	5	7	33
	Shrub	2	2		0	0	0	1
	Total	207	201		1	5	7	34
Remaining species	Tree	213	199		1	13	11	85
	Shrub	43	35		1	7	3	45
	Total	255	233		2	20	14	131
All species	Tree	14 402	13 493		135	773	1 165	5 331
	Shrub	1 872	1 444		101	327	694	2 495
	Total	16 273	14 937		236	1 100	1 859	7 826

*0 signifies a positive amount less than 0,5

In a few cases the independently estimated total biomass does not precisely equal the sum of the constituent biomasses. This is due to one or both of the following reasons depending on species and area: 1, All computer calculations from the application of the allometric formulae onwards were carried out retaining several decimal places. This was to reduce the magnitude of round-off error that would otherwise be propagated during calculation. To obtain minimum round-off error per separate mass category, data were converted to integer form only in the final presentation but this sometimes results in imperfectly additive matrices relative to the last significant digit; 2, For the smallest shrub of some species the estimate of its stem wood mass, through subtraction, becomes marginally negative owing to the predictor variables being applied at the extreme limit of regression range. Such estimates were automatically set to zero as the most feasible estimate of stem wood mass in such individuals. Only where such shrubs occurred in exceptionally large numbers did this setting to zero slightly affect the equality between total biomass and the sum of the constituent biomasses.

Two typographical errors which appeared in the prediction equations of the original report have been corrected. The biomass results remain unchanged.

TABLE 2.—Relative contribution of mass categories for tree- and shrub-sized individuals*

	Trees and shrubs	Trees	Shrubs
Percentage wood biomass	91,8	93,7	77,4
Percentage twig biomass	1,4 (0,9)	0,9 (0,8)	5,4 (2,4)
Percentage leaf biomass	6,8	5,4	17,5
Percentage dead wood mass (of total mass)	10,3 (5,2)	7,5 (5,2)	27,1 (5,0)

* Values in brackets are for all species omitting *Grewia flavescens* as a percentage of total biomass (or of total mass for the bottom line) of the non-*G. flavescens* group.

TABLE 3.—Biomass proportions in the *Burkea africana* population

	Stem wood	Branch wood	Leaf	Twig
Trees	65,5%	29,6%	4,3%	0,7%
Shrubs	24,5%	52,6%	18,7%	4,0%
Total	64,6%	30,1%	4,6%	0,8%

TABLE 4.—Mass and leaf area data for the woody plant component of different areas of the Nylsvley study site

Transect	Size Class	Biomass kg ha^{-1}				Dead Wood Mass kg ha^{-1}	Leaf Area m^2 ha^{-1}
		Total	Stem & Branch Wood	Current twig	Leaf		
A	Tree	17 062	16 029	146	887	1 202	6 153
	Shrub	2 963	2 368	93	502	378	3 941
	Total	20 022	18 397	239	1 388	1 580	10 094
B	Tree	14 767	13 868	135	764	1 155	5 211
	Shrub	1 568	1 187	115	266	925	1 989
	Total	16 335	15 055	250	1 030	2 079	7 200
C	Tree	11 040	10 418	102	520	836	3 652
	Shrub	1 605	1 240	90	277	614	2 063
	Total	12 647	11 658	192	797	1 450	5 715
D	Tree	14 065	13 081	137	847	1 201	5 798
	Shrub	736	510	74	152	649	1 135
	Total	14 800	13 591	210	999	1 850	6 933
E	Tree	15 073	14 069	157	847	1 431	5 841
	Shrub	2 483	1 915	131	438	903	3 346
	Total	17 555	15 984	288	1 285	2 334	9 187
ALL	Tree	14 402	13 493	135	773	1 165	5 331
	Shrub	1 872	1 444	101	327	694	2 495
	Total	16 273	14 937	236	1 100	1 859	7 826

kg ha^{-1} for the abovementioned South West African site although the 20 022 kg ha^{-1} of Nylsvley transect A is in closer agreement. Dayton (1978) found that the biomass of *Combretum apiculatum* and *C. zeyheri,* the two dominant woody plant species in a savanna community in the eastern Transvaal lowveld, was 16 909 kg ha^{-1}. The individuals of these species accounted for about 85% of the woody species crown cover of the community. Kelly & Walker (1976) determined woody plant biomass of nine sites in *Colophospermum mopane* dominated communities in a region with an annual rainfall of approximately 500 mm in south-eastern Zimbabwe. Woody plant biomass ranged from 8 726 to 30 782 kg ha^{-1} and averaged 19 694 kg ha^{-1}. This average value is very similar to the biomass value for transect A of the Nylsvley study site. The relative contributions of the first six ranking species to total woody plant biomass is given in Table 5 for comparison of the Nylsvley site with the South West African site (Rutherford, 1975) and the Zimbabwean site (Kelly & Walker, 1976). The Zimbabwean *C. mopane* site with the median total biomass value was selected for the comparison. It is clear that relative to the other given communities, a considerably greater proportion of the total biomass is unaccounted for by the six major contributing species on the Nylsvley site(s). This relatively lower degree of dominance on Nylsvley is also apparent when compared in terms of basal area to the long-term fire protected *Burkea africana* community seven kilometres from Nylsvley (Rutherford & Kelly, 1978). The relative contribution of shrub biomass to total woody plant biomass for the

Nylsvley site (12%) is virtually identical to the mean proportion (11%) of shrubs given for the Zimbabwean *C. mopane* sites.

The leaf production (1 100 kg ha^{-1}) or shoot production (1 336 kg ha^{-1}) of the Nylsvley site agrees well with data for other savanna areas (Rutherford, 1978), particularly with that of the South West African site. For their *Colophospermum mopane* sites, Kelly & Walker (1976) obtained an average shoot production of 1 506 kg ha^{-1} season $^{-1}$ which is 8% of the mean total biomass. This proportion is identical to that found for the Nylsvley site where shoot production was also 8% of total biomass. For the two dominant woody species in the abovementioned *Combretum apiculatum* and *C. zeyheri* savanna community, Dayton (1978) found shoot production to constitute 9% of the total biomass. On Nylsvlei, the terminal shoot production by the woody species was greater than for example, the

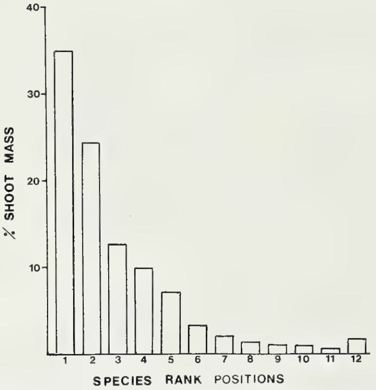

FIG. 2.—Relative contribution of different species to total current season's shoot biomass. Species rank positions are: 1, *Burkea africana;* 2, *Ochna pulchra;* 3, *Terminalia sericea;* 4, *Grewia flavescens;* 5, *Vitex rehmannii;* 6, *Combretum zeyheri;* 7, *Dombeya rotundifolia;* 8, *Combretum molle;* 9, *Strychnos pungens;* 10, *Strychnos cocculoides;* 11, *Securidaca longipedunculata;* 12, remainder.

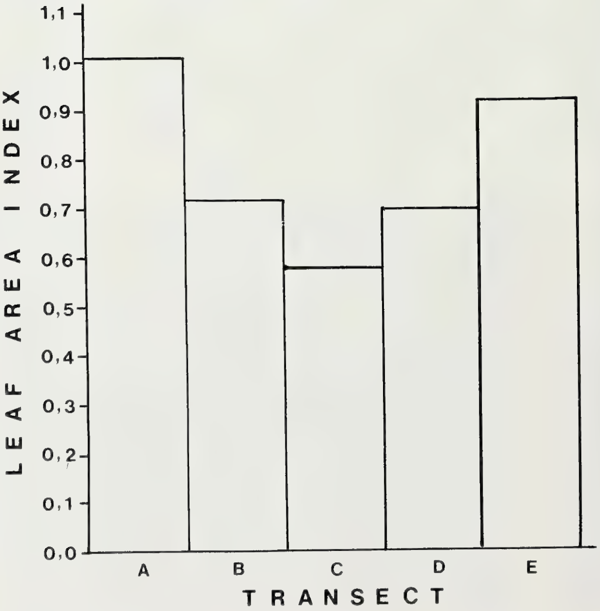

FIG. 3.—Leaf area indices for each transect of the study area.

TABLE 5.—Comparison of species' relative contributions to total woody plant biomass for selected southern African savanna communities (sources in text)

Nylsvley *Burkea africana* community (all transects)			Nylsvley *Burkea africana* community (Transect A)			South West African/Namibian *Burkea africana* community			A Zimbabwean *Colophospermum mopane* community		
Species	Biomass kg ha^{-1}	%	Species	Biomass kg ha^{-1}	%	Species	Biomass kg ha^{-1}	%	Species	Biomass kg ha^{-1}	%
Burkea africana	8 687	53,4	Burkea africana	9 957	49,7	Burkea africana	11 801	52,9	Colophospermum mopane	13 002	60,9
Ochna pulchra	2 136	13,1	Ochna pulchra	3 753	18,7	Terminalia sericea	6 153	27,6	Combretum apiculatum	7 812	36,6
Terminalia sericea	1 734	10,7	Combretum zeyheri	2 066	10,3	Combretum psidiodes	3 405	15,3	Acacia nigrescens	211	1,0
Vitex rehmannii	815	5,0	Terminalia sericea	1 932	9,6	Ochna pulchra	226	1,0	Cissus cornifolia	110	0,5
Combretum zeyheri	691	4,2	Dombeya rotundifolia	521	2,6	Combretum collinum	195	0,9	Dalbergia melanoxylon	100	0,5
Strychnos cocculoides	448	2,8	Grewia flavescens	275	1,4	Securidaca longipedunculata	160	0,7	Commiphora africana	79	0,4
Remainder	1 762	10,8	Remainder	1 518	7,6	Remainder	350	1,6	Remainder	53	0,2
Total	16 273	100,0	Total	20 022	100,0	Total	22 290	100,0	Total	21 367	100,0

peak season herbaceous layer biomass of 1 022 kg ha^{-1} determined on Nylsvley by Grunow in 1975/76 (Huntley, 1977). However, shoot production of the shrub-sized individuals was less than half of this herbaceous layer biomass. For the Zimbabwean *Colophospermum mopane* sites (Kelly & Walker, 1976), mean herbaceous production (1 590 kg ha^{-1}) in an above average rainfall season was slightly greater (6%) than the woody plant shoot production for the same season.

The leaf are index of 0,783 for the woody species is certainly low compared to that of many other vegetation types and even with the addition of the herbaceous layer's LAI, total LAI will probably still be relatively low. Only in transect A does the woody species' LAI just exceed a value of 1. Lieth (1975) indicated a LAI of 1 as the lowest limit for a tropical grassland and states that a wide variety of deciduous communities have leaf area indices of 3 to 6. Leaf area index data from the present study show that the mean LAI of 0,6097 for the whole study area for the *Burkea africana, Ochna pulchra* and *Terminalia sericea* group is slightly lower than a previous Nylsvley estimate of 0,764 in which the enumeration survey sample size was less than one-tenth that used in the present study (Tew & Cresswell quoted in Huntley, 1977). The greatest difference between the two Nylsvley leaf area estimates is for *T. sericea* where the present study indicates LAI to be less than half that found in the earlier study.

The 882 kg ha^{-1} of dead wood (excluding *Grewia flavescens*) is less than the annual terminal production but with *G. flavescens* included, the dead wood mass of 1 859 kg ha^{-1} greatly exceeds annual terminal production. Data on amounts of dead wood mass in other related savanna ecosystems appear to be lacking.

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UITTREKSEL

Bogrondse biomassa word gegee vir elf houtagtige plantsoorte in elk van die vyf strooktransekte wat in die savanne op die Nylsvley studie area bestudeer is. Die gemiddelde bogrondse biomassa vir al die houtagtige plantsoorte was 16 273 kg ha^{-1}, bestaande uit 14 937 kg ha^{-1} hout, 236 kg ha^{-1} huidige seisoenlote en 1 100 kg ha^{-1} blare, asook 'n addisionele 1 859 kg ha^{-1} dooie hout aan die individue. Die plantsoorte wat die grootste bydrae tot die totale biomassa gelewer het, was Burkea africana *(8 687 kg ha^{-1}),* Ochna pulchra *(2 136 kg ha^{-1}) en* Terminalia sericea *(1 734 kg ha^{-1}).* Grewia flavescens *het van die ander plantsoorte verskil deurdat dit 'n proporsioneel groter massa dooie hout en ook 'n groter biomassa van huidige seisoenlote gehad het. Individue van struikgrootte het 11,5% van die gemiddelde totale biomassa en 29,7% van die gemiddelde blaarmassa van al die plantsoorte uitgemaak. Die waardes wat bepaal is in die vyf strooktransekte het aansienlik verskil: die blaaroppervlakte-indeks het byvoorbeeld gewissel van 0,5715 in strooktransek C tot 1,0094 in strooktransek A. Die gemiddelde biomassa-data vir die Nylsvley savanne-studiegebied stem ooreen met beskikbare biomassadata vir savanne-plantegroei elders in Suidelike Afrika.*

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APPENDIX

Prediction equations (statistical variation not obtainable for arithmetically and algebraic equation combinations used for rarer species).

Key: Y = Total biomass (kg)
P = Branch wood biomass (kg)
Q = Current twig biomass (kg)
L = Leaf biomass (kg)
A = Leaf area (m^2)
D = Dead wood mass (kg)
SLA = Specific leaf area (cm^2/g)
$x = \ln [(\text{stem diameter})^2 . \text{height}]$ (cm)
z = stem diameter (cm)
r = correlation coefficient
+ Significant at $P = 0,05$
++ Significant at $P = 0,01$
+++ Significant at $P = 0,001$
$CI_{0,05}$ = Confidence Interval at $P = 0,05$
S_x = Standard error

Burkea africana

$\ln Y = -10,5573 + 1,2018\,x$ $r = 0,993$ +++
$\ln P = -9,9895 + 1,0652\,x$ $r = 0,985$ +++
$\ln Q = -10,2934 + 0,7947\,x$ $r = 0,985$ +++
$\ln L = -9,2845 + 0,8596\,x$ $r = 0,987$ +++
$A = 7,136\,L$ $CI_{0,05} = \pm 0,1602$ or $\pm 2,2\%$; $S_x = 0,081$
$\ln D = -8,4120 + 0,8093\,x$ $r = 0,922$ +++

Ochna pulchra

$\ln Y = -7{,}829 + 0{,}967\,x$ $r = 0{,}989$ +++
$\ln P = -7{,}3749 + 0{,}8003\,x$ $r = 0{,}944$ +++
$\ln Q = -20{,}6788e^{-0{,}2114\,x}$ $r = 0{,}923$ +++
$\ln L = -8{,}08375 + 0{,}76934\,x$ $r = 0{,}980$ +++
$SLA = 87{,}4525z^{-0{,}0715}$ $r = 0{,}7711$ +++
$D = 0{,}00000199e^{1{,}1093x}$ $r = 0{,}919$ +++

Terminalia sericea

$\ln Y = -8{,}1124 + 1{,}0084\,x$ $r = 0{,}988$ +++
$\ln P = -6{,}8060 + 0{,}7845\,x$ $r = 0{,}952$ +++
$\ln Q = -11{,}1603 + 0{,}8169\,x$ $r = 0{,}963$ +++
$\ln L = -8{,}5338 + 0{,}8338\,x$ $r = 0{,}962$ +++
$A = 6{,}115\,L$ $CI_{0{,}05} = \pm 0{,}055$ or $\pm 0{,}9\%$; $S_x = 0{,}028$
$\ln D = -11{,}6215 + 1{,}1274\,x$ $r = 0{,}965$ +++

Strychnos pungens

$\ln Y = -7{,}9002 + 1{,}0116\,x$ $r = 0{,}982$ +++
$\ln P = -8{,}1079 + 0{,}9607\,x$ $r = 0{,}977$ +++
$\ln Q = -11{,}4031 + 0{,}7650\,x$ $r = 0{,}977$ +++
$\ln L = -7{,}1022 + 0{,}6501\,x$ $r = 0{,}978$ +++
$\ln SLA = 5{,}3693 \times {}^{-0{,}1287}$ $r = 0{,}894$ +++
$\ln D = -11{,}5634 + 1{,}0249\,x$ $r = 0{,}904$ +++

Vitex rehmannii

$\ln Y\ 0{,}5 = [\,(-8{,}1124 + 1{,}0084\,x) + (-7{,}9002 + 1{,}0116\,x)\,]$
$\ln Q = -9{,}9334 + 0{,}7947\,x$
$\ln L = -8{,}5338 + 0{,}8338\,x$
$A = 7{,}2\,L$
$D = 0{,}00000199e^{1{,}1093\,x}$

Combretum zeyheri

$\ln Y = -10{,}3373 + 1{,}2018\,x$
$\ln Q = -9{,}4834 + 0{,}7947\,x$
$\ln L = -8{,}9045 + 0{,}8596\,x$
$A = 7{,}3\,L$
$\ln D = -11{,}2734 + 1{,}0249\,x$

Dombeya rotundifolia

$\ln Y = -10{,}7873 + 1{,}2018\,x$
$\ln Q = -9{,}5734 + 0{,}7947\,x$
$\ln L = -9{,}2845 + 0{,}8596\,x$
$A = 6{,}9\,L$
$D = 0{,}00000199e^{1{,}1093x}$

Securidaca longipedunculata

$\ln Y = -7{,}829 + 0{,}967\,x$
$\ln Q$ = same as combined species
$\ln L = 0{,}5\,[\,(-7{,}1022 + 0{,}6501\,x) + (-9{,}2845 + 0{,}8596x)] - 0{,}77$
$A = 7{,}3\,L$
$D = 0{,}00000199e^{1{,}1093x}$

Combined species

$\ln Y = -8{,}5997 + 1{,}0472\,x$
$\ln Q = 0{,}25\,[\,(-20{,}6788e^{-0{,}2114x}) + (-10{,}2934 + 0{,}7947\,x) + (-11{,}1603 + 0{,}8169\,x) + (-11{,}4031 + 0{,}7650\,x)\,]$
$\ln L = -8{,}2511 + 0{,}7782\,x$
$A = 6{,}4\,L$
$\ln D = -11{,}1810 + 1{,}0177\,x$

Bothalia 14, 1: 139–142 (1982)

Annual production fraction of aboveground biomass in relation to plant shrubbiness in savanna

M. C. RUTHERFORD*

ABSTRACT

A new means of estimating the annual production fraction of aboveground biomass of woody plants along a full shrub-tree continuum in savanna is presented. A measure of shrubbiness was found to be quantitatively definable over a shrub-tree continuum, to closely relate to the annual production fraction and to provide a single criterion for defining shrub and tree forms in South African savanna vegetation. It is proposed that in South African savanna, shrubs be defined as perennial woody plants with an annual production fraction of greater than 10% and trees with that less than or equal to 10%.

INTRODUCTION

Data on aboveground plant biomass in certain South African savannas have recently become more readily obtainable. Particularly total aboveground biomass is already known for some areas while in other more shrubby savannas the relative ease of direct total harvesting has been demonstrated. Methods have become more standardized to establish relationships with good correlation between the aboveground dry biomass of the plant and, for example, plant height, stem size and canopy or plant volume (Rutherford, 1979a). These relationships make it possible to determine, with acceptable accuracy, total plant biomass in many areas.

Data on annual production of woody plants are less readily available. Although data on annual shoot (leaf and twig) production are available for some areas of savanna these are more difficult to acquire by harvest owing to labour intensive, time consuming separation and sorting of the parts of the plant canopy. Further difficulty may arise in recognizing current growth of twigs in the absence of bud scar marks (Rutherford, 1979b). Correlation of whole-plant size parameters with the annual production component is sometimes less satisfactory than with total plant biomass.

The annual shoot production is important as a potentially utilizable fraction of plant biomass and renewable browse resource. It is particularly in shrub-sized plants that browse availability increases through an inverse relationship with plant height *per se* and through an increase in the annual production fraction of the plant. The annual production fraction is referred to as APF and is defined as

$$\text{APF} = 100\left(\tfrac{\text{P}}{\text{B}}\right)$$

where P is annual shoot production and B total aboveground biomass without dead branches, and for convenience is expressed as a percentage. Although determined for separate plant individuals, APF is also useful when applied to fairly homogeneous plant stands. APF corresponds approximately to the reciprocal of Biomass Accumulation Ratio of Whittaker (1970) in the form of

$$\text{APF} = \frac{100}{\text{BAR}+1}$$

where BAR is the Biomass Accumulation Ratio.

The objective of the present study was to investigate ways of predicting the Annual Production Fraction of aboveground biomass for woody plants along a full shrub-tree continuum for given savanna vegetation. If possible, prediction was to be considered independent of the plant species studied, to allow for extensive application.

PLANT SHRUBBINESS

It is notoriously difficult to find a commonly acceptable basis for distinguishing between trees and shrubs in many areas of South African savanna. Plant size has often been considered as a measure and applied in different ways (Edwards, 1976; Van der Meulen, 1979). Various measures of stem size have been used effectively for biomass relations, but become impracticable to apply in multi-stemmed shrubs. Plant volume, computed as a cylinder in cubic meters, is more easily applied to both trees and shrubs. One formula is

$$\text{V} = \left[\frac{\text{D}_1 + \text{D}_2}{4}\right]^2 \pi\text{H}$$

where V is plant volume, D_1 and D_2 long and short axis canopy diameters and H plant height. The concept of 'shrubbiness' of a plant involves more than plant size and requires consideration of additional factors.

Consider Whittaker's (1970) ranges of Biomass Accumulation Ratios for different terrestrial biome types and the conversions to Annual Production Fraction in Table 1. The terrestrial biome types corresponding to South African woody savannas are shrublands and woodlands. From the data it is clear that the Annual Production Fraction increases with a transition from woodlands to shrublands. It appears that some measure of how shrubby a woody savanna plant is, that is, its 'shrubbiness', is required to associate with this transition. General associations are that shrubbiness, although subject to the genetic constraints of the species concerned, normally increases with past fire treatment and with aridity but is inversely related to plant age. Shrubbiness of a plant

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TABLE 1.—Biomass Accumulation Ratio and Annual Production Fraction according to terrestrial biome type (After Whittaker, 1970)

Terrestrial Biome Type	Biomass Accumulation Ratio	Annual Production Fraction (APF %)
Desert	2 — 10	9,1 — 33,3
Grassland	1,5 — 3	25,0 — 40,0
Shrubland	3 — 12	7,7 — 25,0
Woodlands	10 — 30	3,2 — 9,1
Mature Forests	20 — 50	2,0 — 4,8

is affected by number of leader shoots and stems of the plant and it is relevant that in many South African savanna types, single stemmed plants are usually a special case of the multi-stemmed norm. These considerations appear to point to a basis for defining shrubbiness quantitatively and to providing for a continuum from distinct forms of shrubs to those of trees. The essence of shrubbiness is taken to be that which increases with number of growing leader shoots but decreases with increase in plant height. Number of basal stems often correlate positively with the number of leader shoots so that a Shrubbiness Index (SI) is given by

$$SI = C - \ln\left(\tfrac{H}{N}\right)$$

where H is plant height in centimeters and N the number of basal stems. The constant C is set to 7 so that the SI value increases with increased shrubbiness and allows for one-stemmed trees up to about 11 m height. These largest trees have, therefore, a Shrubbiness Index defined as zero. The current limits of application are based on the data collected and are discussed below. Wiens & Rotenberry (1981) relate shrubbiness to the amount of plant material in the 0,3 to 0,6 m height interval. This measure appears restricted to a range of smaller shrubs and is probably not suited to a shrub-tree continuum.

METHOD

Twenty generally deciduous plants ranging from distinct tree forms to distinct shrub forms were destructively sampled after completion of their seasonal shoot growth in three of Acocks's (1975) Veld Types. These were Mixed Bushveld, Arid Sweet Bushveld and Kalahari Thornveld in the Transvaal. Shrubs were particularly well represented in the two last mentioned more arid types. A range of plant species was sought and included *Acacia tortilis* (Forssk.) Hayne subsp. *heteracantha* (Burch.) Brenan, *Burkea africana* Hook., *Combretum apiculatum* Sond. subsp. *apiculatum*, *C. zeyheri* Sond., *Dombeya rotundifolia* (Hochst.) Planch., *Grewia flava* DC., *G. flavescens* Juss., *G. monticola* Sond., *Mundulea sericea* (Willd.) A. Chev., *Ochna pulchra* Hook., *Peltophorum africanum* Sond., *Tarchonanthus camphoratus* L. and *Terminalia sericea* Burch. ex DC. Plant height varied from 0,5 to 11,0 m. Measurements taken were vertical plant height (H), long and short axis canopy diameter (D_1; D_2) and count of number of basal stems (N). All current season's shoot growth was clipped and total plant and shoots weighed excluding dead branches. Subsamples were taken for dry mass (at 85°C) conversion of data. Basal stem counts did not include branches that originated more than 0,1 m above ground level nor that originated above 5% of plant height in smaller plants less than two metres tall. On plants greater than 1,5 m tall, fine basal coppice shoots less than 5 mm in diameter at base were sampled for weighing but were excluded from the stem count.

RESULTS AND DISCUSSION

Plant size in the form of plant volume, as defined above, was found to relate exponentially to the Annual Production Fraction (Fig. 1) but with a correlation coefficient less than 0,90. Greatest variation in the relation occurred in smaller plants with volume of less than about 6 m^3. An essentially no better relationship was obtained by first relating plant volume to total plant biomass (r = 0,99), then to annual shoot production (r = 0,89) and dividing the one regression formula by the other. Plant volume appears to be unsatisfactory for more precise estimation of Annual Production Fraction.

The components of the Shrubbiness Index (SI) are given graphically in Fig. 2 and the limits of application indicated. The data do not necessarily apply to plants less than 0,5 m height, plants with more than 80 countable basal stems, geoxylic suffrutices or tall polycormic trees. The present data and unpublished

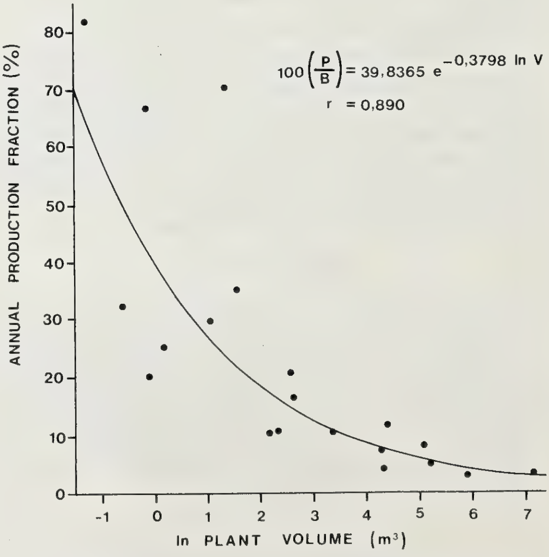

FIG. 1.—Relationship between plant volume and annual production fraction where $100\ (\frac{P}{B})$ is annual production fraction and V is plant volume and r is correlation coefficient.

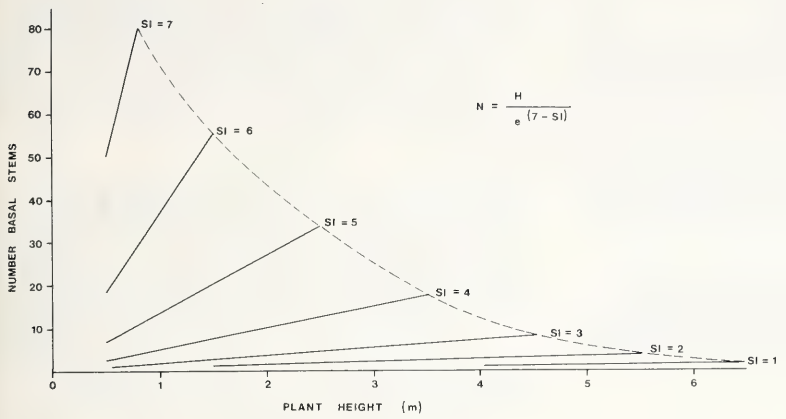

FIG. 2.—Relationships between plant height (H) and number of basal stems (N) for shrubbiness indices (SI) from 1 to 7, number of stems from 1 to 80 and plant height from 0,5 to 6,5 m. Valid application is limited to the area to the left of the broken line.

observations and tests have shown that occurrence of plants that correspond to positions in the upper right section of the graph is rare. Any plants that do occur in this area usually cause an overestimation of the Annual Production Fraction when applied as described below. All plants included have at least one stem and plants more than 7 m high usually have only one stem.

Shrubbiness Index related closely to Annual Production Fraction with a correlation coefficient of 0,964 (Fig. 3). This is a considerably improved exponential relation compared to that using plant size particularly in the range of smaller plants. A hypothetical example of use of information from both Figs 2 & 3 illustrates the method. For a given area of fairly uniform vegetation, a mean plant height of 2,8 m and 5 basal stems per plant gives a Shrubbiness Index of 3 which in turn results in an expected Annual Production Fraction of 16%. With a known total biomass of say 10,0 tons/ha this results in an annual shoot production estimate of 1,6 tons/ha/year. It is important to note that for very low Shrubbiness Index values, small differences between estimated and actual Annual Production Fraction (data points show APF as low as 3% when 5% is predicted in Fig. 3) when applied to a tall tree can make a relatively large difference to the estimate of absolute annual shoot production.

The asymptotic trend of the limits of application of the Shrubbiness Index with increasing height in Fig. 2 (uppermost height range not shown) indicates that a Shrubbiness Index value of about 2 may be a convenient delimiter of shrubs and trees in the abovementioned veld types. This points to a definition of shrubs and trees based on a single measure namely the Annual Production Fraction (APF) of the plant and conveniently be set at 10% (corresponding to SI of 1,9). It is therefore proposed that shrubs be defined as those perennial woody plants with an APF greater than 10% and trees as those with an APF of less than or equal to 10%. From this definition and Fig. 2 it follows that in terms of plant height, shrubs can extend to about five and a half metres tall, whereas the lower height limit of trees lies between one and a half and two metres. Outside these two height limits, woody plants are either exclusively shrubs or trees. The Annual Production Fraction of 10% for distinguishing between shrub and tree forms is somewhat higher than the APF of 7,7 to 9,1% indicated by Whittaker (1970) to separate shrublands from woodlands. The Annual Production Fraction of the present study is aimed at the plant individual and not at averages for heterogeneous vegetation. It is for this reason also that the range of APF in this study is far greater than that for Whittaker's (1970) biome types (Table 1). The following correspondences may assist in providing a word picture of Shrubbiness Index values for individual plants: SI of 0 to 1, mainly larger savanna trees; SI of 1 to 2, mainly smaller savanna trees; SI of 2 to 5, majority of common shrubs; SI of greater than 5, mainly smaller shrubs with very many stems.

The use of the SI-APF relationship for the projection of shrub growth forwards of backwards in time is complex and depends on the degree of constancy of basal stem number, the rate of change in

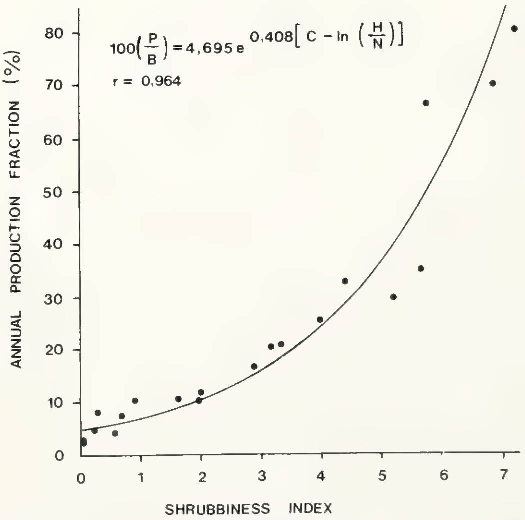

FIG. 3.—Relationship between shrubbiness index and annual production fraction where P is annual production, B is biomass, 100 $\left(\frac{P}{B}\right)$ is annual production fraction, C is 7, H is plant height, N is number of basal stems and r is correlation coefficient.

plant height and the large and variable deciduous leaf component of shoot production.

The sample size in the present study remains small. Although it encompasses plants of different ages and species with different management treatments from different areas and savanna Veld Types, the Shrubbiness Index-Annual Production Fraction relation should be tested and applied over further variation in savanna to determine its full extent and applicability in South African savanna as a whole.

ACKNOWLEDGEMENTS

I am indebted to Mr M. D. Panagos for major assistance in the field and to Mr R. H. Westfall and Dr D. Edwards for helpful suggestions in the text.

UITTREKSEL

'n Nuwe metode vir die beraming van die jaarlikse produksie gedeelte van bogrondse biomassa van houtagtige plante vir 'n volledige struik-boom kontinuum in savanna word gegee. Daar is gevind dat 'n struikagtigheidsmaat kwantitatief definieerbaar is oor 'n volledige struik-boom kontinuum, nou verband hou met die jaarlikse produksie gedeelte en dien as 'n enkele maatstaf om struik- en boomvorms in die Suid-Afrikaanse savanna plantegroei te definieer. Daar word voorgestel dat in Suid-Afrikaanse savanna, struike as meerjarige houtagtige plante met 'n jaarlikse produksie gedeelte van meer as 10% en bome met dié van minder of gelyk aan 10% gedefinieer word.

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Miscellaneous ecological notes

VARIOUS AUTHORS

CORRECTIONS TO ACOCKS'S 'VELD TYPES OF SOUTH AFRICA' (1975)

It has been pointed out to me by Ms S. J. Milton of Tugela Ferry, Natal, that the last column of figures in Table 1, p. 11, of the second edition of Acocks's 'Veld types of South Africa' *(Mem. bot. Surv. S. Afr.* 40, 1975) is incorrect. Unfortunately the errors arose in the conversion to metric. The last column should read as follows:

Number of plants per hectare
15 122 520
1 680 280
746 791
420 070
186 698
105 018
67 211
37 806
26 254
11 669
2 917
729
467
263
117
42
19
7
2
1

It is suggested that botanists possessing this memoir should xerox the column above and paste it over the offending column, since it is of the same format.

In addition, there is an error on p. 78, column 1, line 3: the figure mentioned should be 51 800 square km and not 32 000 square km.

D. J. B. KILLICK

REVIEW OF THE WORK OF THE BOTANICAL RESEARCH INSTITUTE, 1980/1981

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INTRODUCTION

Progress with the important Flora of Southern Africa project gives cause for satisfaction, in spite of the limited manpower available. Particularly gratifying was the progress with taxonomic research on the mosses, pteridophytes and fossil plants.

As in past years the publication effort of the Institute was substantial — a total of 95 individual publications. Apart from scientific publications, pamphlets on 18 of the most important waterweeds were published in both Afrikaans and English. The National Weeds List comprising some 1 600 species is almost ready for publication.

Two important ecological projects were started, namely a survey of the Transvaal forests and a study of 35 Cape estuaries.

The Biennial General Staff Meeting was held in Pretoria from 19–21 August 1980. It was attended by nearly all staff including staff from the units and proved very successful (Fig. 1). Officers reported on their research projects and each report was followed by a brief discussion. On the last day the Director, Dr B. de Winter, spoke on 'Rationalization and the future'.

REPORTS OF THE SECTIONS

HERBARIUM SERVICES SECTION

The four herbaria of the Institute continued to identify plants and provide information for a wide range of people including officers of the Institute, various State and Provincial Departments, universities and the public both in South Africa and its neigbouring states.

National Herbarium, Pretoria (PRE)

A total of 14 395 specimens was named and 519 visitors dealt with. Accessions to the herbarium numbered 14 357. During the year 41 loans (4 775 specimens) were sent out to other Institutes while 34 loans (2 620 specimens) were received for study. A total of 61 loans (9 027 specimens) was returned to PRE by borrowers. We received 663 specimens on exchange and 6 465 as gifts but did not distribute any duplicates during the year.

Once again due to lack of rain in the western half of the country, no major expeditions were undertaken. However, the good late rains localized in the southern Orange Free State and adjacent northern Cape produced some good collections especially new records for grasses.

Expansion of the herbarium is taking place rapidly. To house the ever-increasing number of specimens 150 of the modular steel cabinets are on order for delivery in mid 1981.

The herbarium/s data bank system, PRECIS, which has been partially in operation this year, has proved to be too cumbersome and costly in its operation. The whole matter of herbarium maintenance, data bank operation and information retrieval are being carefully re-examined. A simplified and more manageable data bank system, PRECISELLA, is being planned and hopefully should be in operation by the end of 1981.

Among the numerous visitors who came to consult the collections and staff were the following: Prof. D. and Dr. U. Müller-Doblies (Berlin), Prof. H. D. Ihlenfeldt and party (Hamburg), Dr. C. Puff (Vienna), Dr. Juliet Prior (London: Swaziland Archaeological Association), Mr P. Karis and Miss B. Nilsson (Stockholm), Mr L. C. Leach (Salisbury Zimbabwe).

Wing A: Mrs E. van Hoepen continues to control the Wing in a part-time capacity while controlling the information and identification service.

Miss C. Reid is continuing with a preliminary revision of the genus *Tetraria* (Cyperaceae).

Miss L. Smook is continuing to co-operate with overseas researchers on a revision of *Vulpia.* The work of the late Dr P. Auquier of Liege has been taken over by Dr C. A. Stace of Leicester. She is also planning, under the guidance of Dr G. E. Gibbs Russell, a booklet on the grasses of the Transvaal and has begun to make a record of all the common names applied to grasses.

Wing B: Mr G. Germishuizen should complete his revision of the southern African members of the Polygonaceae by the end of 1981. The text for the new book on Transvaal Wild Flowers with paintings by Anita Fabian was completed. The book should appear in print by the end of the year.

Mrs L. du Toit joined the herbarium during the year and is currently working herself into the early families of dicotyledons. She replaced Mr B. D. Schrire, who had been transferred to Durban.

The herbarium's data bank encoders are housed in this wing. Their work involves the encoding of accessions and the checking of computer entries and printouts. The spirit collection of 3 050 bottled specimens is also housed in this wing.

Wing C: Miss E. Retief is continuing her research in the Campanulaceae with a revision of *Lightfootia* and *Wahlenbergia.*

Mr Herman should complete his anatomical investigation of *Pavetta* (Rubiaceae) by the end of 1981. This will assist the research team at the University of Pretoria with its revision of the southern African species. He is also continuing with his investigations in the seed and fruit collection towards a long-term project aimed at an identification guide to the seed and fruit types found in southern Africa. Miss Retief and he are jointly producing a poster paper on this subject for the AETFAT Congress.

Mr E. G. H. Oliver continues to work on the Ericaceae in between his administrative duties and is preparing a paper on a reassessment of the subfamily Ericoideae for the AETFAT Congress.

Mr C. J. Hildyard is currently doing his 3rd year botany course for his B.Sc. degree at the University of Pretoria.

Wing D: Miss W. G. Welman continues as the regional extractor for Exerpta Botanica (Taxonomica) and with various administrative duties.

Mrs S. J. Smithies has assisted at various times with literature work for the palaeobotanical section due to her expertise in the subject.

Mrs K. A. Kleynhans left the herbarium in January 1981 and was replaced by Mrs W. le Grange.

Cryptogams: The establishment of the separate cryptogamic wing in the basement has proved very successful not only for the additional space and facilities but also for the consolidation of the collection in the packeted system in roll-out card index cabinets. Repacketing of the whole collection will soon be complete with the last stages of repacketing of lichens taking place. The lichen collections on rocks will be housed in the herbarium cabinets which were redesigned for the fossil collection. These should arrive in mid 1981.

A total of 4 009 moss specimens was sent out on exchange and only 248 specimens were received. Loans sent out consisted of 89 specimens and loans received for study of only 41 specimens.

Dr R. E. Magill completed the first fascicle of the volume on Bryophyta for the Flora of Southern Africa. The manuscript includes an introduction on the mosses, a glossary and the text that treats 191 species in 60 genera and 12 families. Research on the second fascicle is well advanced. His goal is to have this fascicle in press by the next annual review. Only preliminary research has so far been undertaken on the families in fascicles 3 and 4. Only provisional identifications are presently done for specimens collected for these groups.

Dr Magill is assisted by Mr J. van Rooy who is finalizing his revision of *Bryum.* He should also obtain his B.Sc. degree through the University of South Africa by the end of 1981.

Mr F. A. Brusse has spent most of his time curating the lichen collection. He went on a short field trip to the northern Transvaal and at the end of the period was accompanied by Dr Knox of the University of the Witwatersrand on a month's collecting trip to the drier parts of the south-western Cape. Mr Brusse obtained his M.Sc. degree from the University of the Witwatersrand for his thesis on *Xanthoparmelia.*

Services: Mrs S. M. Perold has been operating the Hitachi SEM in the examination of plant material for several taxonomists. She also assists Dr Magill with bryophyte research.

Mrs G. L. Radmacher was engaged in the determination and plotting of grid references for some 1 935 species of the Cape flora using records from all the major herbaria. For this purpose Miss D. Frost and Mr A. Linder Snr were employed in Cape Town. The distribution patterns will be analysed by computer for a paper to be presented to the AETFAT Congress by Mr E. G. H. Oliver, Mr H. P. Linder Jnr and Dr J. P. Rourke of Kirstenbosch. This work is the beginning of a long-term project to record the distribution of all taxa occurring in the Cape floral region.

Natal Herbarium, Durban (NH)

A total of 1 127 specimens was named and 391 visitors dealt with. Among the latter were student and school groups. Accessions to the herbarium numbered 967. Some 1 495 specimens in 8 loans were sent out for study.

Mr B. D. Schrire was transferred to the herbarium from Pretoria at the beginning of the period. He and Mrs B. J. Pienaar and Mrs L. Nichols spent much time in updating the herbarium. He also saw to the cleaning up of the rather overgrown garden area. He began investigating the Desmodieae (Fabaceae) for a thesis to be registered at the University of Durban-Westville for an M.Sc. degree.

Mrs Pienaar concentrated on updating and improving the cultivated exotic collections mainly from the fine neighbouring Municipal Botanic Gardens.

Miss B. M. Sassen left after six years as the clerical assistant and was replaced by Mrs Young.

Albany Museum Herbarium, Grahamstown (GRA)

A total of 1 686 specimens was named and 498 visitors and 2 groups of 64 students dealt with. The accessions to the herbarium numbered 1 184. Some 11 loans of 333 specimens were sent out, 1 964 donations were received.

Mrs E. Brink continues to run the herbarium and deal with the information service. Dr Amy Jacot Guillarmod has been appointed in a part-time capacity to assist with curatorial and information matters.

The staff dealt with 40 botanical displays in the Museum during the year and continued to administer the Grahamstown Nature Reserve.

Government Herbarium, Stellenbosch (STE)

The number of specimens named totalled 5 226 with 350 visitors requiring information. Accessions to the herbarium numbered 4 005. In all 13 loans of 425 specimens were sent out to researchers.

Miss L. Hugo continues as curatrix of the herbarium which is experiencing considerable pressure for identifications from the increasing ecological activity in the Cape fynbos.

Mrs C. M. van Wyk (Née Schonken) completed her revisionary work in *Pelargonium* and obtained her M.Sc. degree at the University of Stellenbosch.

Mr D. Davies left the herbarium at the beginning of 1981 and moved to the University of Cape Town as a research assistant. His place was taken by Mrs A. C. Fellingham.

Much of the routine herbarium procedure has been effectively streamlined by Mrs R. M. Wikner.

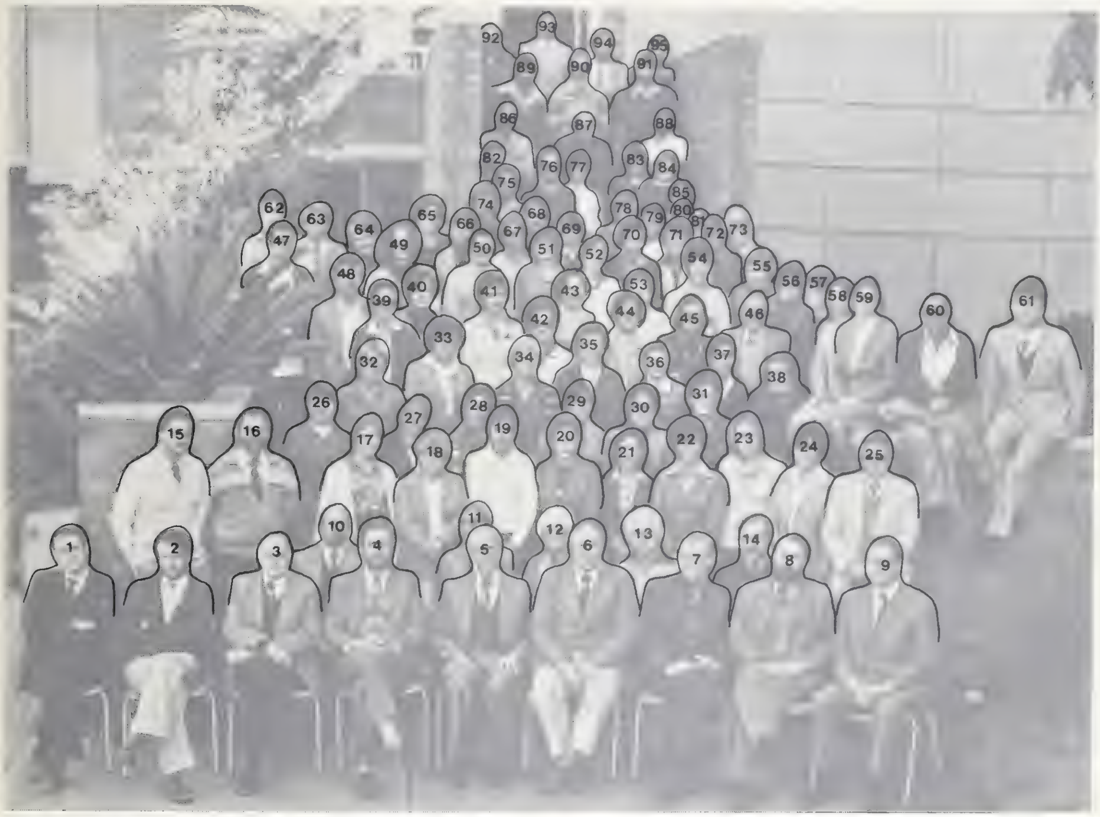

FIG. 1.—Staff of the Botanical Research Institute on the occasion of the Biennial General Staff Meeting, 19–21 August 1980. 1, Dr J. W. Morris; 2, Mr R. P. Ellis; 3, Dr L. E. W. Codd; 4, Dr D. J. B. Killick (Deputy Director); 5, Dr B. de Winter (Director); 6, Dr D. Edwards (Assistant Director); 7, Mr H. C. Taylor; 8, Mr M. J. Wells; 9, Dr J. C. Scheepers; 10, Dr O. A. Leistner; 11, Mrs E. Brink; 12, Dr I. C. Verdoorn; 13, Mrs A. A. Mauve; 14, Mr E. G. H. Oliver; 15, Mr T. H. Arnold; 16, Dr R. E. Magill; 17, Mrs S. Smit; 18. Mrs E. van Hoepen; 19, Mrs J. Mulvenna; 20, Mrs N. Miller; 21, Mrs V. M. Engelbrecht; 22, Mrs B. A. Momberg; 23, Mrs L. du Toit; 24, Miss E. Retief; 25, Mr D. F. M. Venter; 26, Mrs M. J. A. W. Crosby; 27, Miss C. Reid; 28, Mrs B. F. Lategan; 29, Mrs E. Ebersohn; 30, Miss W. G. Welman; 31, Mrs A. M. Verhoef; 32, Miss C. A. Liengme; 33, Mrs C. F. Fourie; 34, Mrs J. Gerke; 35, Mrs R. M. Wikner; 36, Miss E. N. Pare; 37, Mrs C. M. van Wyk; 38, Mrs P. W. van der Helde; 39, Miss C. E. Smith; 40, Mrs I. J. Joubert; 41, Mrs L. R. Filter; 42, Mrs K. A. Kleynhans; 43, Mrs S. M. Perold; 44, Mrs M. M. Loots; 45, Mrs D. M. C. Fourie; 46, Mr A. Smith; 47, Mr B. Curran; 48, Mr B. D. Shrire; 49, Miss K. L. Immelman; 50, Mrs J. H. Jooste; 51, Mrs N. Nigrini; 52, Mrs M. C. van Niekerk; 53, Mrs A. M. Fourie; 54, Mrs J. Rautenbach; 55, Mrs C. A. Bester; 56, Mrs J. I. M. Grobler; 57, Mrs M. E. M. Venter; 58, Dr G. E. Gibbs Russell; 59, Mrs S. J. Smithies; 60, Mr A. A. Balsinhas; 61, Dr P. J. Weisser; 62, Mr P. van Eden; 63, Mr H. J. de Villiers; 64, Mrs I. R. Leistner; 65, Mrs R. Botha; 66, Mrs E. Evenwel; 67, Mrs J. B. Hoffmann; 68, Mr J. van Rooy; 69, Mrs A. J. Engelbrecht; 70, Mrs G. E. Hussem; 71, Mrs S. M. Thiart; 72, Mrs A. D. Bronkhorst; 73, Miss E. Boon; 74, Mr G. Germishuizen; 75, Mr D. A. Davies; 76, Mr C. H. Stirton; 77, Mrs A. Gill; 78, Mr C. F. Musil; 79, Miss N. van der Meulen; 80, Miss K. J. Duggan; 81, Mrs K. P. Clarke; 82, Miss L. Henderson; 83, Miss R. J. Parsons; 84, Miss B. C. Radmacher; 85, Mrs. Q. L. Radmacher; 86, Mr R. H. Westfall; 87, Mr J. Erens; 88, Mr G. B. Harding; 89, Mr T. A. Ankiewicz; 90, Mr. J. Conradie; 91, Mr G. B. Deall; 92, Mr F. A. Brusse; 93, Mr C. Boucher; 94, Dr M. C. Rutherford; 95, Mr B. M. Campbell.

FLORA RESEARCH SECTION

The section encompasses taxonomists and palaeotaxonomists with assistants and artists. Its major task is the production of the Flora of Southern Africa, the Palaeoflora of Southern Africa as well as regional floras.

Flora of Southern Africa

Two works are in press and are expected to appear during 1981. The first of these is an introductory volume written by Miss M. D. Gunn and Dr L. E. Codd with the title Botanical Exploration in Southern Africa. It consists of two parts, the first dealing with botanical exploration from early historical times to the middle of the 18th century, while the second part is an encyclopedia of past and present plant collectors who have worked on the subcontinent. The second work in press is a fascicle in the Cryptogam series dealing with the families Sphagnaceae to Grimmiaceae of the mosses written by Dr R. E. Magill.

Good progress was made in the following volumes by members of staff. Work by other taxonomists submitted to the editor is also mentioned.

Vol. 2: In the course of preparing this volume on the estimated 1 000 species of grasses Dr G. E. Gibbs Russell is well advanced with a register of names and types of Poaceae. Currently there are about 3 000 names in the register and it is estimated that a further 1 500 will be added. Keys to the species of 11 tribes, including Andropogoneae have been completed and the write-up of the small tribe Meliceae was finished. The genus *Ehrharta* was sorted into taxa.

Vol. 3: For this volume on Cyperaceae Mr T. H. Arnold and Miss C. Reid have continued their studies on the large genus *Ficinia.*

Vol. 4: Mrs A. A. Mauve put finishing touches to the 42 species of the families Xyridaceae, Eriocaulaceae, Pontederiaceae and Juncaceae. The sculpturing of the seed surface provided taxonomically important characters. Apart from a revision of the genus *Aneilema* in the Commelinaceae work on the second fascicle of this volume is now complete.

Mr H. P. Linder who is stationed at the Bolus Herbarium of the University of Cape Town has begun work on the family Restionaceae which will form the first fascicle of this volume.

Vol. 5: Liliaceae. The genera *Urginea* and *Drimia* of the tribe Urgineae are being revised by Mrs A. A. Mauve. In most members of these genera leaves and flowers are produced at different times of the year. Consequently most specimens, including the types, are incomplete. The two genera together will probably account for about 35 species of which about 10 are new. The four species of the genus *Tenicroa,* formerly called *Sypharissa,* were written up for Bothalia by Mrs A. A. Mauve who also prepared a short note on some members of the genus *Bulbine.*

Vol. 6: Amaryllidaceae. Mrs A. A. Mauve worked on some problems in the genus *Cyrtanthus* and described a new species of *Strumaria.*

Vol. 7: *Iridaceae.* Prof M. P. de Vos of the University of Stellenbosch has adapted her revisions of the genera *Romulea* and *Syringodea* to Flora format and has submitted them to the editor. Mrs A. A. Mauve described a new species of *Gladiolus,* a genus of which she published a complete southern African revision some years ago.

Vol. 8: Orchidaceae. Mr H. P. Linder prepared revisions of several genera including *Disa, Herschelia* and *Monadenia* for publication in Contr. Bolus Herb. and Bothalia. The published revision of *Eulophia* by Dr A. V. Hall of the Bolus Herbarium is being converted into Flora format.

Vol. 10: Mr G. Germishuizen has completed the taxonomy of the 18 species of *Polygonum* in the region.

Vol. 11: Dr H. F. Glen, the present Liaison Officer of the Royal Botanic Gardens, Kew, has continued his studies of *Ruschia* and *Apatesia* and of the type specimens of other genera of the Mesembryanthemaceae.

Vol. 14: Crassulaceae. Dr H. R. Tölken, formerly of the BRI, now at Adelaide, South Australia, has made progress in adapting his *Crassula* revision to Flora format.

Vol. 15: A revision of the genus *Rubus* (Rosaceae) by Mr C. H. Stirton is more than half completed.

Vol. 16: For part 3 of this volume on Fabaceae a revision of *Eriosema* was almost completed for publication in Bothalia by Mr C. H. Stirton, and 27 species of *Psoralea* were written up and a revision of *Rhynchosia* is well under way. Mr B. D. Shrire has begun studies in the tribe Desmodieae.

Vol. 18: Revisions of the genera *Kirkia* (Simaroubaceae) and *Triaspis* and *Acridocarpus* of the Malphigiaceae were completed by Miss K. Immelman. *Triaspis* was reduced from eight species to two, one with three subspecies.

Vol. 21: Dr I. C. Verdoorn has prepared *Melhania* and *Dombeya* (Sterculiaceae) for publication in Bothalia.

Vol. 25: Ericaceae. Mr E. G. H. Oliver rounded off a revision of *Philippia* for publication in Bothalia.

Vol. 28: Dr L. E. Codd described two new species of *Plectranthus.*

Vol. 30: Miss K. Immelman has started on a revision of *Justicia* (Acanthaceae).

Vol. 32: Miss E. Retief has continued her studies of *Wahlenbergia* and *Lightfootia* (Campanulaceae).

Algae: A catalogue of green, brown and red marine algae completed by Prof S. C. Seagrief of Rhodes University, Grahamstown is being edited for publication as an ancillary volume.

Bryophyta: Dr R. E. Magill has begun work on fascicle 2 of part 1 of his account of the mosses.

Pteridophyta: Prof E. A. Schelpe of the Bolus Herbarium, University of Cape Town, is preparing a volume on the 250 species of ferns and fern allies found in the region. He has submitted texts of 180 species including some of the larger genera such as *Asplenium, Marsilea* and *Cheilanthes.*

Palaeoflora of Southern Africa

Two collecting trips to important localities in the Molteno Formation were undertaken by Drs J. M. and H. M. Anderson. One-and-a-half tons of fossiliferous shale were collected and processed. This resulted in nearly 2 000 catalogued slabs which were added to the Institute's Molteno collection which now totals almost 7 000 specimens. These collections led to significant improvements being made in the revision of the genus *Dicroidium* which is being prepared for the Palaeoflora.

The review of genera of megaplants of the Permo-Triassic which is produced under the editorship of Drs J. M. and H. M. Anderson has progressed well. Thirty experts from all parts of the world are contributing to this work.

Register of plant taxonomic projects

The register was updated with the aid of a questionnaire sent out in collaboration with the secretariat of AETFAT (l'Association pour l'étude taxonomique de la flore d'Afrique tropicale).

Southern African Plants — waterweeds

In the series Southern African Plants, which is published as a continuation of Farming in South Africa, pamphlets on 18 of the most important waterweeds were published in both English and Afrikaans. Two or more colour photos show the plant in its habitat, from close-by and in detail. A distribution map gives South African records. The text consists of a brief, image-creating description in non-technical language. A paragraph on related species contrasts the species to other members of its genus while a section on distribution discusses briefly distribution and dispersal. A short paragraph on ecology is followed by notes on importance, legislation, control and the origin of the name. A list of publications consulted concludes each brochure. Species dealt with include kariba weed *(Salvinia molesta),* parrots' feather *(Myriophyllum aquaticum)* and water hyacinth *(Eichhornia crassipes).*

Pretoria Flora

Keys and descriptions of 680 species belonging to 49 families were finalized and typed. Among the larger families dealt with were Cyperaceae (92 species), Orchidaceae (42 species), Euphorbiaceae (44 species), Malvaceae (33 species), and Rubiaceae (32 species). Family descriptions were designed to be, as far as possible, image-creating and diagnostic. A key to all tree species, based on vegetative characters, was largely completed. Copies of many keys were distributed inside and outside the Institute for testing.

Ceropegia *and related genera*

An account of the genera *Ceropegia, Riocreuxia* and *Brachystelma* has been completed by Dr R. A. Dyer. It covers the same ground as Vol. 27,4 of the Flora of Southern Africa written by the same author. It is, however, fully illustrated, in some cases by colour plates, provides many distribution maps and is written for both the botanist and the amateur.

Liaison Officer, Kew

The current incumbent of the post, Dr H. F. Glen, continued to provide information services to the BRI and to other institutes and researchers in many parts of the world. His research was mainly directed towards the genera *Ruschia* and *Apatesia* of the Mesembryanthemaceae. Particular emphasis was placed on numerical taxonomy.

PLANT STRUCTURE AND FUNCTION SECTION

After 18 months of being understaffed this section once again has a full staff complement with the appointment of Mr J. J. Spies as cytogeneticist and the return of Mrs R. Botha (nee Manders) after secondment to university and the Data Processing Section. In addition Miss H. Botha and Miss A. Alberts have been appointed to provide technical assistance in the laboratory.

Comparative grass leaf anatomy

This project has progressed satisfactorily and Mr R. P. Ellis concentrated on the eragrostoid grasses. Successful collecting trips were undertaken to Zululand, the Kalahari and the Kruger National Park where rare grasses such as *Schoenefeldia transiens, Lintonia nutans, Heterocarpha schiemaniana* and *Alloteropsis papillosa* were found. The anatomy of these and other eragrostoid species indicate that several species and genera in this sub-family appear to be incorrectly classified and several taxonomic adjustments may be necessary to reflect relationships more accurately.

Grass identification by epidermal structure for herbivore food preference studies

Mrs R. Botha has initiated this study in an attempt to quantify the diet of grazing herbivores. Factors that affect this quantification will be examined and for this purpose samples of three widespread grass species *(Themeda triandra, Brachiaria serrata, Eragrostis capensis)* have been collected at different localities in South Africa. Various anatomical epidermal characteristics, as well as possible differences in digestibility, that may be influenced by environmental factors, are being studied.

Cytogenetics

Mr J. J. Spies, whose main interest lies in the cytogenetics of the genus *Sorghum,* recently joined this section. He has undertaken a short study to determine whether a correlation exists between the surface area of the stomatal complexes and the chromosome number in *Eragrostis curvula.* The results were interesting in that an increase in chromosome number was found to be positively correlated with an increase in stomatal surface area. These results imply that this method of measuring stomatal areas can be applied to the identification of diploid *E. curvula* plants. These diploids are rare, sexually reproducing plants that many represent ancestral populations and they are essential for any breeding programme that may be contemplated.

ECOLOGY SECTION

The function of the Ecology Section is to study the vegetation of South Africa and its ecological relations. This work involves three main aspects:

- The identification, description, classification and mapping of the various kinds of vegetation.
- Study of the ecological relationships between different kinds of vegetation — with each other and with the environment — and of the various processes and mechanisms that determine the behaviour of plant communities.
- The application of ecological knowledge and methods to environmental planning.

Veld types of South Africa

Further progress on the revision of the veld types of the western half of the country is being made as a co-operative venture, involving Institute staff and also people outside the Institute. That part of the revised treatment of the Kalahari Thornveld that remains to be completed awaits the completion of the revision of the veld types of the Northern Cape, on which considerable progress is being made by Mr A. Gubb of the McGregor Museum, Kimberley.

Transvaal bushveld survey

Field work on the plant ecology of the farm Groothoek, Thabazimbi District, has been completed by Mr R. H. Westfall. The vegetation has been classified into 21 communities and variations of communities. The condition of the vegetation has also been assessed. The synthesis of community, habitat and assessment data is reflected in a single table that was prepared by a new set of computer programmes developed for this purpose.

Transvaal forest survey

Preparatory work on a transect study in the Sabie area is well under way with air-photo interpretation and stratification for stratified random sampling having been completed by Mr G. B. Deall. He has commenced field sampling.

KwaZulu coastal dune survey

Dr P. J. Weisser has completed field work for the project 'Vegetation study of the Zululand coastal dunes between Richards Bay and Mlalazi Lagoon'. He has collected specimens and recorded vegetation data from about 120 sites. Areas important for conservation were found mainly along the coast, near to the Mlalazi River Mouth and the vicinity of the new Richards Bay Mouth.

Studies of littoral vegetation

In a special study of the coast vegetation opposite St Croix Island near Port Elizabeth, extending about 18 km along the coast and about 4 km inland, Mr H. C. Taylor distinguished five major vegetation categories: (1) *Scaevola thunbergii* Pioneer Vegetation of littoral dunes and *Ficinia lateralis* Sedgeland of calcrete gravel; (2) *Olea exasperata* Bush, *Pterocelastrus tricuspidatus* Bushclumps and Dune Woodland; (3) Sundays River Scrub; (4) Fynbos of calcrete areas and (5) *Themeda triandra* Grassland. Invasion of the area dy *Acacia cyclops* is becoming severe.

Further work is being done for the book on dry coastal ecosystems (in Elsevier's series *Ecosystems of the World*) on a co-operative basis with co-workers not on Institute staff. From various published and unpublished sources, Dr P. J. Weisser has contributed to a section on the dune vegetation of the east coast of South Africa. Meanwhile, Messrs C. Boucher and H. C. Taylor have nearly completed work on the western and southern Cape coast. In this phytosociological study, confined to the special vegetation that comes under the direct and strong influence of the sea and the maritime climate, Mr Taylor distinguishes a series of five major plant communities from wet to dry, along the southern Cape coast. Of these, two occur on bedrock, one on limestone and two on marine sand. The simple pioneer dune community is the most widespread, but since all five communities are represented in most of the landscape segments of the coastline, he concludes that this strand vegetation comprises only one floristic element.

Analysing data previously collected along the western Cape coast, Mr Boucher shows that the strand vegetation between Table Bay and the Orange River mouth can be divided into the Capensis and the Namaqualand Floristic Regions, with the Olifants River mouth as boundary. He distinguishes three groups of communities in the Namaqualand and two in the Capensis strand regions. A nature reserve along the Namaqualand coast is an urgent priority because extensive opencast diamond mining is destroying large tracts of vegetation.

Studies of Cape estuaries

After completing preparatory work, Miss R. J. Parsons commenced field work on a botanical survey of the 138 Cape estuaries between the Orange and Kei Rivers in September 1980. She has mapped the vegetation of 35 estuaries from colour aerial photographs and, for 11 of these, the mapping units have been checked and their species composition, structure and environmental conditions studied.

Aquatic ecology

Mr C. F. Musil has synthesized field and laboratory data on the growth rate and chemical composition of water hyacinth plants and he is preparing a final report on his results and their implications. Growth co-efficients determined in culture compare favourably with those determined for various species of diatoms and algae. Growth rates in the field are considerably higher than those in culture, but are influenced by the growth form of plants, atmospheric conditions and nutritional factors. Provided lower growth rates determined in culture are compensated for, growth co-efficients generated in culture can be used to predict growth rates measured in the field.

Using air photos, Dr P. J. Weisser and Miss R. J. Parsons studied the increase of reeds *(Phragmites australis)* from 1937 to 1976 in the Siyai Lagoon in Natal. The reeds increased from 0,27 ha in 1937 to 2,94 ha in 1976.

Cape fynbos survey

Western Cape foreland studies

Mr C. Boucher has prepared a preliminary vegetation map of the western foreland between the Berg River mouth and False Bay showing the boundaries of the Strandveld, Coastal Fynbos and Coastal Renosterveld vegetation types at a scale of 1: 250 000. He subdivides these veld types into twelve smaller categories. He has also altered some accepted veld type boundaries particularly near Saldanha Bay and the Cape Flats.

By 1972, agriculture, urbanization and the spread of introduced weeds had reduced the former extent of Strandveld, Coastal Fynbos and Coastal Renosterveld, south of the Berg River, to 41%, 14% and 6% respectively. Only 0,2% of the original extent of Strandveld in the western foreland is conserved, and only 0,01% of Coastal Fynbos and of Coastal Renosterveld. Therefore there is a very urgent need to preserve remnants of these veld types.

Cape mountain fynbos studies

Mr B. M. Campbell has completed his field sampling and data processing towards setting up a structural-functional classification of mountain fynbos that is much needed by managers and researchers working in this vegetation. A classification has been developed that has been tested in the field and is now being finalized. Several papers are being prepared on various aspects of this work.

Orothamnus zeyheri *(marsh rose)*

Observations by Mr C. Boucher over an extended period have revealed that marsh rose populations show cyclical fluctuations in size depending on the length of the inter-fire interval. The longer the interval, the fewer the number of remaining plants. This species could survive a fire-free period of 34 years although a fifteen-year period would probably be optimal.

Frequent fires, excessive trampling and an increase of infestations of *Phytophthora cinnamomi* or other lethal fungi can endanger the survival of this threatened plant of mountain fynbos.

Fynbos biome project

As an initial contribution to this project, Mr C. Boucher has examined the vegetation of the Fynbos Biome Project study site at Pella. Eight communities were identified and a preliminary map was drawn. The final map, together with a systematic checklist of the flora will be completed when further identifications are received.

NAKOR national plan for nature conservation

With the indispensable assistance of Miss B. K. Drews and, latterly, of Mrs R. Müller, Dr J. C. Scheepers has continued to act as part-time co-ordinator to the NAKOR National Plan for Nature Conservation for the Department of Water Affairs, Forestry and Environmental Conservation. The latter Department will henceforth provide the services of a full-time co-ordinator, while the Institute will, for the time being, provide the technical support necessary to manage the data bank and related operations.

Other environmetal planning work

Miss B. K. Drews has prepared a report on the vegetation of the P160-1 highway corridor, planned to pass through the Magaliesberg and Witwatersrand Ranges. In this report, possible impacts that the highway might have on the surrounding vegetation are discussed and recommendations made as to how these could possibly be minimized. On the basis of air-photo interpretation and information received from Saasveld Forestry Research Station, she has recommended the setting aside of certain natural areas in the George Guide Plan, which is being prepared by the Environmental Conservation Branch of the Department of Water Affairs, Forestry and Environmental Conservation.

South African savanna ecosystem project

During his studies on the seasonal biomass change of the dominant woody species at the Nylsvley study site, Dr M. C. Rutherford has investigated important departures from the normal sigmoidal growth pattern in shoots of selected woody plants. Early season growth fluctuations could be largely ascribed to asynchronous growth of shoot populations as well as to the dependence of different conversions to shoot mass through time. Shoot growth was also affected significantly by plant size and the branched status of the twigs. Root studies of savanna plants showed that the hitherto unknown rate of root tip loss was fairly constant during the growing season but attained a maximum in autumn and winter.

PLANT EXPLORATION SECTION

Research in this section, under the leadership of Mr M. J. Wells, has been divided mainly between weeds and plant utilization research. With the recent establishment of the Weeds Research Unit, this Institute's involvement with weeds research has largely fallen away. This section will therefore have most of its energy directed at investigating the more useful elements of our flora. One of the priority areas will be the conservation of germ plasm, particularly of the primitive crop plants many of which have serious, man-made selective pressures rapidly aiding their disappearance.

Conservation of germ plasm

This project has progressed slowly with all its input coming from activities carried out in other projects. Its fundamental aim is to conserve the germ plasm of primitive crop plants. Over the year 33 collections were made of *Lagenaria,* collected mainly in Zululand and Gazankulu. Other collections include *Sorghum* and *Pennisetum* 11, *Citrullus* 5, Pulse crops 10 and miscellaneous 19.

Conservation of threatened plants

Originally covered by the germ plasm project, this project has now been given independent status with Mrs J. B. Hoffmann as the responsible officer.

The rare and endangered plants of the Transvaal (216 taxa) were examined and the compilation of dossiers for each taxon started. Each dossier will house all available information about individual threatened taxa. Based on a list of taxa in the National Herbarium, represented by 5 or less collections, an additional ± 480 taxa were added to the Threatened plants list increasing the total to ± 2 395 taxa. Threatened plants growing in the BRI gardens and nursery were also listed. These comprise 40 families, 113 genera and 261 species. Of these 3 taxa are considered to be extinct in the wild *(Encephalartos woodii, Leucadendron concavum* and *Elephantorrhiza woodii),* 14 endangered, 50 vulnerable, 106 rare, 37 indeterminate and 51 uncertain.

Origin and classification of sorghum

Approximately 100 specimens of primitive crop Sorghums collected throughout South Africa were examined by Mr T. H. Arnold and identified to the level of race and in some instances to forms. Forty-one collections many from elsewhere in Africa were obtained from the Department's seed bank and have been grown. A review was made of all available archaeological literature pertaining to *Sorghum* in South Africa. This has revealed from recent carbon datings of *Sorghum* seed that this crop probably arrived in South Africa 700 years earlier than originally estimated, namely about 1 700 BP. (± 200 AD).

Origin and classification of pennisetum

Miss K. J. Duggan's work on primitive crop Pennisetums has shown that the cultivated members of this genus are extremely variable. In some parts of the country it is often difficult to find two inflorescences from a single field looking alike. Despite this, most of the material examined appears to belong to *Pennisetum americanum* subsp. *americanum* race *typhoides* (cultivated type). A limited number of specimens were identified as belonging to *P. americanum* subsp. *stenostachyum* (weedy type). Club-shaped inflorescence forms reported not to exist in South Africa have been collected from various localities. Two new morphological characters not mentioned in existing literature were discovered. The exact importance of these characters has not yet been established.

Ethno-botany

In her wood utilization study by the Tsonga of Gazankulu Miss C. A. Liengme has weighed and analysed 192 bundles of firewood. The most important species used are *Colophospermum mopane* and *Combretum apiculatum,* representing 41% and 21% of the total firewood weight recorded. Mopane also comprises 90% of the wood utilized in hut and granary construction. During a period of 6 months 87 huts were built in the study area of three villages. Each hut requires 30–46 poles and this means that between 2 610–4 002 poles were used. One hut pole often represents one tree. However, assuming that two poles are produced by a single tree, then anything up to ± 2 700 trees were removed from the vegetation during the six month period.

Tree distribution in the Transvaal

The basic field work towards establishing high resolution distribution maps of each of the 900 indigenous woody species of the Transvaal has progressed significantly. Dr J. M. Anderson has sampled a further 174 of the 1/16th degree square units thus completing his sampling contribution. Other non-institute contributors will require a further summer season in order to bring the field work to a close. It is estimated that a further 2–3 years' work will be required to bring the tree atlas to completion. Two significant additions to the proposed format include the autecological element being enhanced and the inclusion of pen sketches for each species. This work has already begun.

Barrier plants

Progress here has been good. Miss L. Henderson has added ± 30 species to the existing security barriers list, bringing the total to 230 species. Five basic elements have been recognized within the various forms of barriers. These elements may in some cases form a barrier alone, but in most cases work best when in combination with each other. The plants which best satisfy the barrier requirements of each element must possess 5 or 6 characteristics which are used to define each element. Ninety species have so far been assessed and allotted to one of the 5 barrier elements. Based on a point system associated with each characteristic, the species examined have been given priority (suitability) ratings within each element.

One hundred different taxa have been collected on field trips, either as whole plants or cuttings, and are being grown in the institute nursery. Similarly the seed germination tests have been carried out on 20 taxa.

Information service

Mrs D. M. C. Fourie, our Scientific Information Officer, handled 477 requests for information about economic plants and their utilization or control. These include 133 identifications of cultivated plants, 90 telephone enquiries and 254 information requests to post.

With the help of Mrs Hoffmann numerous visitors

(1 897), including Science Olympiad winners, overseas visitors, scholars and members of the public were taken on special tours of the Institute and its gardens and nursery.

Mrs Fourie is also playing a very active role in organizing the menu for the special indigenous dinner to form part of the AETFAT congress to take place in Pretoria during January 1982.

National weeds list

The basic weeds list compiled by Mr A. A. Balsinhas now includes the names of some 1 600 species. A weed classification system has been devised by Mrs V. M. Engelbrecht. The classification system covers the origin, habitat, kinds of weeds, weedy characteristics, useful characteristics, life cycle, reproduction, growth form and woodiness (in addition to a taxonomic classification and common names). To date, ± 1 280 species have been classified.

Lantana camara

Thirty taxa have been written up and photographed by Mr C. H. Stirton so far. Each taxon has been assigned a uninomial e.g. sheba, baxa, jabula, quagga, etc. Preliminary field keys have been compiled for all the yellow- and the orange-flowering taxa, and tested in the field. The remaining keys and taxa will be completed in 1981/1982. Flowers, fruits, stems and leaves of four taxa have been surveyed with the SEM and show taxonomically significant differences. This work is being continued.

Rubus

Up until Mr C. H. Stirton's return from Kew, plants of *Rubus* were housed in various greenhouses within the BRI. These have all been repotted, fertilized, relabelled, and placed in a central shade house. Specimens have been photographed and prepared for examination using the scanning-electron microscope.

Nassella tussock

The investigation into the longevity of nassella tussock by Mr M. J. Wells has been shelved until autecological work being carried out by Mr D. Joubert (E. Cape) and Mr G. B. Harding (Winter Rainfall) are completed. As both these officers do or will fall under the Weeds Research Unit and are better placed to carry out field work, it is now envisaged that this project will later be taken over by one of them.

Woody invaders

In the Transvaal 41% of the ¼ degree squares in the survey area have been sampled by Misses Henderson and Duggan. Of this figure 31% were completed this year. Forty-eight species, including five additions to the list, have been recorded. Of these 12 are considered to be particularly aggressive and invasive.

Leguminosae

Considerable progress has been made in defining the species limits of *Psoralea* in South Africa. Types of most species have now been traced. Mr C. H. Stirton has also written up detailed description of 18 species of *Psoralea* and *Otholobium,* 3 species of *Rhynchosia,* and one species of *Rafnia;* five being new species. Mr Stirton has also registered for a Ph.D at the University of Cape Town, the subject of his thesis being 'A revision of African Psoraleae', and will be studied using the principles of cladistic analysis and vicariance biogeography.

GARDEN SECTION

A total of 1 420 accessions, including 606 research accessions of material of *Lantana, Lagenaria, Sorghum* and other genera, was received and classified and catalogued during the year. The area surrounding the new dams was landscaped. Road construction continued and normal replacement plantings of annuals and shrubs were made in the garden. Five hundred and eighty-eight trees were transplanted from the nursery to the six biomes. The post of Curator is still vacant. In the meantime, Mr H. J. de Villiers and Mr D. S. Hardy are Acting Curators of the garden and nursery respectively.

BOTANICAL RESEARCH INSTITUTE

Scientific, Technical and Administrative Staff
(31st March 1981)

Director

B. de Winter, M.Sc., D.Sc. (Taxonomy of Poaceae, especially *Eragrostis,* and of *Hermannia;* plant geography)

Deputy Director

D. J. B. Killick, M.Sc., Ph.D., F.L.S. (General taxonomy, nomenclature, mountain ecology and editing)

Assistant Director
(Agricultural Research Leader)

D. Edwards, M.Sc., Ph.D. (Ecological methodology, aquatic plants, remote sensing, vegatation structure and physiognomy)

ADMINISTRATION

Administrative Officer	D. F. M. Venter
Senior Administrative Assistant	Mrs G. E. Hussem, B.A.
Senior Administrative Assistant (Personnel)	J. Conradie
Assistant Accountant	Mrs J. Rautenbach
Administrative Assistants	Mrs D. J. Gerber Mrs M. C. van Niekerk Mrs. S. J. Smit* (Assistant to Assistant Director)
Personal Secretary to Director	Mrs M. M. Loots
Senior Clerical Assistant	Mrs T. Creffield (Registry)
Clerical Assistants	Mrs C. A. Bester Mrs P. Bruggeman* Mrs. I. J. Joubert* (Registry) Miss H. van Zyl
Receptionist	Mrs M. E. M. Venter
Typists	Mrs S. S. Brink Mrs J. Gerke* Mrs N. Miller* Mrs S. M. Thiart*
Technician: Assistant to Secretary-General: AETFAT	Mrs B. A. Momberg, B.Sc.*

HERBARIUM SERVICE SECTION

Officer in Charge	E. G. H. Oliver, M.Sc.

NATIONAL HERBARIUM, PRETORIA (PRE)

Agricultural Researchers	E. G. H. Oliver, M.Sc. (Curator; Ericaceae) Mrs E. van Hoepen, M.Sc. (Assistant Curator; supervision of identifications and enquiries)
Senior Administrative Assistant	Mrs J. Mulvenna

Wing A (Cryptogams—Monocotyledons)

Agricultural Researchers	Mrs E. van Hoepen Miss C. Reid, B.Sc. Hons
Research Technician	Miss L. Smook, B.Sc. (Poaceae)
Technical Assistant	Mrs A. M. Fourie*

Wing B (Piperaceae—Oxalidaceae)

Agricultural Researchers	G. Germishuizen, B.Sc. Hons (Polygonaceae) L. du Toit, B.Sc. Hons
Technical Assistant	Mrs I. R. Leistner*

Wing C (Linaceae—Asclepiadaceae)

Agricultural Researchers	Miss E. Retief, M.Sc. (Campanulaceae) P. P. J. Herman, B.Sc. Hons
Research Technician	Mrs M. J. A. W. Crosby, B.Sc.*
Technical Assistants	Mrs J. I. M. Grobler* C. Hildyard, B.Sc. (Elec. Eng.) (part-time)

Wing D (Convolvulaceae—Asteraceae)

Agricultural Researchers	Miss W. G. Welman, M.Sc. Mrs S. J. Smithies, M.Sc.
Technical Assistant	Mrs W. la Grange*

Cryptogamic Herbarium

Agricultural Researchers	R. E. Magill, M.S., Ph.D. (Musci) F. A. Brusse, M.Sc. (Lichens)

---

* Half day.

Technical Assistants	Mrs. L. R. Filter* Mrs P. W. van der Helde J. van Rooy (Musci)

Services

Research Technician	Mrs S. M. Perold, B.Sc.* (S.E.M. and laboratory work)
Technical Assistants	Mrs I. Ebersohn (Herbarium records, loans and exchanges, etc.) Mrs G. L. Radmacher (Grid references and phytogeography) Mrs D. Frost (stationed at Bolus Herbarium) A. Linder* (stationed at Bolus Herbarium)
Typist	Mrs A. M. Verhoef
Laboratory Assistants	J. Phachla (Mounting) W. Kgaditsi (Preparation and packing)

Data Bank

Technical Assistants	Mrs E. Evenwel* Mrs J. H. Jooste* Mrs N. Nigrini* Mrs W. Roux*

Photographic Room

Photographer................	Mrs A. J. Romanowski

NATAL HERBARIUM, DURBAN (NH)

Agricultural Researcher	B. D. Shrire, B.Sc. Hons (Curator; Fabaceae and general identifications)
Research Technician	Mrs B. J. Pienaar, B.Sc.
Technical Assistant	Mrs L. Nichols
Clerical Assistant...........	Miss B. M. Sassen

ALBANY MUSEUM HERBARIUM, GRAHAMSTOWN (GRA)

Agricultural Researcher	Mrs E. Brink, B.Sc. (Curator; general identifications)
Research Technician	Mrs A. F. M. G. Jacot-Guillarmod, M.A., M.Sc., D.Sc.
Technical Assistants	Vacant Miss G. V. Britten*
Laboratory Assistant	A. Booi

GOVERNMENT HERBARIUM, STELLENBOSCH (STE)

Agricultural Researchers	Miss L. Hugo, M.Sc. (Curator; general identifications) Miss C. M. van Wyk, M.Sc.
Research Technicians	D. A. Davies, B.Sc. Mrs A. C. Fellingham, B.Sc.
Technical Assistant	Mrs R. M. Wikner
Clerical Assistant...........	Miss E. N. Pare
Laboratory Assistant	J. Ambraal

FLORA RESEARCH SECTION

Officer in Charge...........	O. A. Leistner, M.Sc., D.Sc., F.L.S.

FLORA OF SOUTHERN AFRICA TEAM

Agricultural Research Leader	O. A. Leistner, M.Sc., D.Sc., F.L.S. (Taxonomy, especially Malvaceae)
Agricultural Researchers	J. M. Anderson, Ph.D. (Palaeoethnobotany, palaeoflora, plant geography) L. E. W. Codd, M.Sc., D.Sc. (Taxonomy, especially Lamiaceae; history of plant collecting) Mrs G. E. Gibbs Russell, B.Sc., Ph.D. (Taxonomy, especially grasses) H. F. Glen, M.Sc., Ph.D., F.L.S. (Numerical taxonomy, Mesembryanthemaceae) Miss K. L. Immelman, M.Sc. (Taxonomy) H. P. Linder, M.Sc. (Taxonomy, especially Orchidaceae and Restionaceae) Mrs A. A. Obermeyer-Mauve, M.Sc. (Taxonomy, especially monocotyledons)
Research Technician	Mrs H. M. Anderson, Ph.D. (Palaeoflora)
Graphic Artists	Mrs R. C. Holcroft* Miss C. E. Smith*
Technical Assistants	Mrs C. F. Fourie
Pupil Research Technician	Miss C. J. Odendaal

PLANT STRUCTURE AND FUNCTION SECTION

Agricultural Researchers	R. P. Ellis, M.Sc. (Anatomy of southern African grasses) Mrs R. Botha, B.Sc. Hons (Food prefer-

	ence studies of grazing herbivores) J. J. Spies, M.Sc. (Cytogenetics of *Sorghum* and *Lantana*)
Technical Assistant	Miss H. Botha
Pupil Research Technician	Miss A. Alberts

ECOLOGY SECTION

Officer in Charge	J. C. Scheepers, M.Sc., D.Sc.

Regional Studies

Agricultural Research Leader	J. C. Scheepers, M.Sc., D.Sc. (Vegetation ecology, especially of forest/woodland/grassland relationships; phytogeography)
Agricultural Researchers	C. Boucher, M.Sc. (Lowland fynbos and phytosociology; conservation and land-use planning; Braun-Blanquet approach and techniques) G. B. Deall, B.Sc. Hons (Vegetation ecology of forest/-woodland/grassland inter-relationships) D. J. McDonald and phytosociology; Braun-Blanquet approach and techniques) C. F. Musil, M.Sc. (Aquatic ecology and survey of aquatic plants, especially in Natal; ecophysiological studies on *Eichhornia crassipes* and *Salvinia molesta*) H. C. Taylor, M.Sc. (O/C Botanical Research Unit, Stellenbosch; mountain fynbos and forest ecology; Braun-Blanquet approach and techniques; conservation) R. H. Westfall, B.Sc. Hons (Ecology and phytosociology of Transvaal Bushveld)
Research Technicians	Mrs A. J. Engelbrecht, B.Sc. (Ecological data processing and presentation; ecological literature; nature conservation; air-photo interpretation and cartography) Mrs A. E. McDonald, B.Sc. (Fynbos ecology and phytosociology; applied ecology). Mrs J. Schaap, H.P.E.D. (Draughtsmanship and cartograpy; artwork, layout and design)
Pupil Research Technician	Miss A. Breytenbach

Environmental Ecology

Agricultural Researchers	P. J. Weisser, Ph.D. (Reedswamp ecology; ecological planning and environmental impact studies; Zululand coast dune vegetation; conservation) Miss B. K. Drews, B.Sc. Hons (Applied ecology and environmental planning; conservation) Miss R. J. Parsons, B.Sc. Hons (Estuarine ecology and phytosociology)
Research Technician	Mrs R. Müller, B.Sc. (Ecological planning and environmental studies; conservation)

Experimental Ecology

Agricutural Researchers	M. C. Rutherford, M.Sc., Ph.D., Dipl. Datamet. (Biomass and production studies in woodland and fynbos ecosystems; competition and stress in fynbos ecosystems) Miss F. M. Pressinger, B.Sc. Hons (Ecophysiological studies in fynbos; competition and stress in fynbos ecosystems)
Research Technicians	B. Curran, B.Sc. (Ecological instrumentation and field studies)

	M. D. Panagos, National Diploma in Agriculture (Botanical Research). (Biomass and production studies in woodland ecosystems; data processing and computer science)

PLANT EXPLORATION SECTION

Officer in Charge	M. J. Wells, M.Sc.
Agricultural Research Leader	M. J. Wells, M.Sc. (Weeds research, botanical horticulture, fynbos utilization and conservation)
Agricultural Researchers	T. H. Arnold, M.Sc. (Plant utilization, taxonomy of crop plants — *Sorghum,* conservation of germ plasm, and threatened indigenous plants) Miss K. J. Duggan, B.Sc. Hons (Conservation of germ plasm, woody exotic invaders, *Pennisetum)* G. B. Harding, B.Sc. Hons (Weed research) Miss L. Henderson, B.Sc. Hons (Cover and barrier plants, woody exotic invaders) Miss C. A. Liengme, B.Sc. Hons (Ethnobotany) C. H. Stirton, M.Sc. (Taxonomy of weeds and related indigenous taxa)
Research Technicians	Mrs V. M. Engelbrecht, B.Sc. (Weeds research) Mrs D. M. C. Fourie, B.Sc. (Scientific information service, identification of exotics) Mrs J. B. Hoffmann, B.Sc. (Public relations and conservation of germ plasm)
Technical Assistants	A. A. Balsinhas (Plant collecting) P. van Eden (Ethnobotany)
Pupil Research Technician	L. Killian (Weeds research)

PRETORIA NATIONAL BOTANICAL GARDEN

Curator	Vacant
Acting Curator (garden)	H. J. de Villiers
Acting Curator (nursery)	D. S. Hardy
Agricultural Research Technicians	H. J. de Villiers, NTC (Hort.). Dipl. Rec. P.A. (Development of savanna biome) D. S. Hardy (Nursery supervision, succulents and orchids)
Agricultural Research Technicians	T. A. Ankiewicz, Dip. For. (Administration, stores and purchases, and development of coastal forest biome) J. Erens (Propagation of display material)
Technical Assistants	Miss K. Behr, B.Sc. (Garden utilization and research collections) Mrs K. P. Clarke (Garden records) Mrs B. C. de Wet* B.A. (Garden records)
Pupil Research Technicians	Vacant Vacant
Farm Foremen	H. N. J. de Beer G. J. Stolz
TN 4 Supervisor	L. C. Steenkamp

PUBLICATIONS BY THE STAFF (1 April 1980–31 March 1981)

1. **Scientific**

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2. **Popular**

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Leistner, O. A. ET AL., 1980. Fennel-leaved pondweed (*Potamogeton pectinatus* L.), *Fmg S. Afr., South African Plants* W2/1980.

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Book Reviews

Die Natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigsten Arten, insbesondere den Nutzpflanzen. Volume 28bI Angiospermae: Order Gentianales, fam. Loganiaceae. Ed. A. J. M. Leeuwenberg. *Berlin: Duncker & Humblot.* 1980. Pp. viii + 255, 170 × 245 mm, 30 plates, 65 figures. Price DM 188,00.

This is the first volume of Die Natürlichen Pflanzenfamilien to be published in English. It is also the first time that several specialists from different disciplines have made separate contributions to one volume.

The work comprises the following chapters: (1) General discussion of relationship between the taxa inside and with taxa outside the family, written jointly by most of the authors of the volume; (2) Taxonomy by Leeuwenberg and P. W. Leenhouts; (3) Vegetative architecture by F. Hallé; (4) Anatomy of the secondary xylem by Alberta M. W. Mennega; (5) Pollen morphology by W. Punt; (6) Embryology by M. I. Hakki; (7) Cytology by Th. W. J. Gadella and (8) Phytochemistry and (9) Useful plants by N. G. Bisset. There is also a foreword by the general editors, an introduction by the editors, an introduction by the editor of the volume and indices of plant names and of plant constituents.

The classification by Leeuwenberg does not differ fundamentally from that of Solereder who wrote up the family for the first edition about 90 years ago, but the treatment is innovative in several respects. The Loganiaceae as circumscribed here, is heterogeneous and old (essentially older than the break-up of Gondwanaland). Numerous previous authors had split it into several families, Hutchinson into as many as eight. Leeuwenberg, along with Leenhouts, chooses to see unity in diversity. He places such odd-men-out as *Desfontainia, Plocosperma* and *Retzia,* as well as the Buddlejeae (with scrophulariaceous leanings) firmly into the loganiaceous fold. He expresses the hope that the 'present monograph will provide enough evidence for it to be generally accepted that they[1] (the genera here placed in Loganiaceae) 'should be left there'. It appears from the joint chapter on relationship that the specialists from the other disciplines had no basic objections to the proposed classification. Some may, however, have regarded it as a compromise as the relationships suggested by their findings are at variance in several cases either with those of the taxonomist or with those of one or more of the other specialists.

The ten tribes are arranged in a sequence meant to reflect their affinity. The same applies to the 29 genera and presumably to the species of which the majority is listed under the genera. There are only four short to very short keys in the work, one to the genera and to two of the four sections of *Buddleja,* one to the wood anatomy of most of the genera and two very brief ones in the chapter on pollen morphology. The parallel genus key 'is entirely artificial and its sole purpose is to enable the name of the genus to which a plant belongs to be determined in the easiest possible way'. Such a key may be easier to use than the 'natural' indented keys of the first edition but it does not provide a quick overview of the important diagnostic characters. There is no key to the sections of *Strychnos* or *Buddleja.* Gone are the species keys of earlier volumes which had the reader searching for Greek and other letters or symbols indicating the next contrast somewhere in the body of the text. Some of the species can of course be identified with the help of this volume. Firstly, those in monotypic genera, furthermore those depicted on the 35 excellent, and mostly full page, line drawings showing a representative of each genus, and a few more can be tracked down through their wood anatomy. But then, most species have been dealt with in recent to very recent monographs written largely by Leeuwenberg and Leenhouts themselves.

Chapter 3 on vegetative architecture is brief, with four pages of text and nine drawings and photographs. In the 18 genera discussed 12 qualitatively different models are distinguished. As the author states 'it is too soon to draw any taxonomic conclusions' from the present findings. The wood anatomy of 24 genera representing 9 of the tribes is dealt with in a chapter of 49 pages including 17 excellent photographic plates and a key. The treatise provides much information of relevance to the taxonomist. The same is true of the chapter on pollen morphology. Representatives of all tribes and their relationships are discussed. The photos again are excellent. The consistent spelling of *Buddleja* with an 'i' on Figure 5,1 may take the reader back to the good old days. Embryologically the family is not yet well-known but the available data on the 8 genera investigated to date is well summarized. Roughly 20 per cent of the c. 470 species of Loganiaceae have been studied cytologically. It is not a 'cytologist's family' as the chromosomes are mostly small and show no marked differences in shape, either within the same complement or between those of different species. Polyploidy is relatively frequent and up to 456 chromosomes have been found in *Buddleja.* Phytochemically the Strychneae is for obvious reasons by far the best known tribe and its treatment occupies more than half the pages of the chapter on the subject. In the tradition of chemists literature references are cited by means of numbers and not by author and date. In his conclusion Bisset briefly discusses phytochemical relationships and the anomalous chemistry of *Buddleja* within the family. The same author provides a short review of useful plants. Verdcourt's book on Common poisonous plants of East Africa is not cited; but then, poisonous plants may only be useful to some. Furthermore, Kokwaro's work on Medicinal plants of East Africa, which is referred to, contains a reference to Verdcourt's book.

The language editor should have been a bit stricter, especially in the chapter on embryology. But overall the volume is produced to the high, exacting standards of this classic work. With its relatively large print and ample spacing the average number of words per page is noticeably less than in previous parts, while the price per page, even taking into account the inflation rate, seems to be higher than ever before.

The editors are congratulated on the production of this volume. Many botanists will be looking forward to the next one.

O. A Leistner

Thonner's Analytical Key to the Families of Flowering Plants by R. Geesink, A. J. M. Leeuwenberg, C. E. Ridsdale & J. F. Veldkamp. (Leiden Botanical Series, Volume 5). *The Hague/Boston/London: Leiden University Press.* 1981. 225 × 150 mm, pp. xxvi + 231, 1 photo, 3 plates. Price Dutch guilders 69,00 (cloth) 38,50 (paper).

The Identification of Flowering Plant Families, including a key to those native and cultivated in north temperate regions, 2nd edn, by P. H. Davis & J. Cullen. *Cambridge: Cambridge University Press.* 1979. 185 × 124 mm, pp. 113, 8 figures. Price R6,65 (paper).

Both these books are, at least in a sense, second editions and both were written with students of botany in mind. Davis and Cullen dedicated the first edition to their students and they have gone to great lengths to make their book as useful and self-contained as possible. The Austro-Dutch book could be considered somewhat less of a student's friend. Geesink and his three co-workers are aware of this and they start their readers off with the consoling warning that 'all plants are hybrids' (obviously a debatable statement), to which they add somewhat irreverently, 'but some are greater bastards than others'.

Davis and Cullen present a completely revised edition of a work which first appeared in 1965. The number of families included in the keys was increased from 260 to 272, the indented keys of the first edition were changed to the bracketed type 'as students seem to find this type of presentation easier to use', the taxonomic system employed is that of Stebbins and no longer that of Benson, and both text and family descriptions have been revised and enlarged. The book consists essentially of four parts: an introduction in which terms and abbreviations used are explained and hints are given on how to examine a plant; this is followed by 37 pages of keys with a short introduction on how to use them; the third part comprises 31 pages with very concise and abbreviated descriptions of 256 families, and the work ends with a brief chapter on further identification, a glossary of 8 pages and an index to families and higher groups.

The work by the four botanists from Leiden and Wageningen began as a translation into English of the Anleitung zum Bestimmen der Familien der Blütenpflanzen, 2nd edn (1917, Berlin: Friedländer) by Franz Thonner, an Austrian 'Privatgelehrter' (scholar of independent means). It soon became obvious that much more than a translation was called for, and this is what the four have accomplished: All families (about 350) and segregate families (about 200) given in the 8th edition of Willis (1973) and in the third edition of Hutchinson's Families of flowering plants (1973) have been accounted for and the 812 key couplets in the original work of Thonner's have been increased to a staggering 2 117. The new Thonner consists largely of one enormous key covering the best part of 194 pages. This is accompanied by a brief account of Thonner's life and work, notes on using the key, a glossary of 15 pages, including a few drawings, and an index to all taxa mentioned in the key.

Why update a key that was devised more than 60 years ago? We are told that Thonner's Anleitung has been extensively used at Dutch universities for many years and, in the opinion of the four authors, it has proven to be the most reliable work of its kind. They admit that its complexities may have scared off even professional botanists, who then had to take recourse to other, simpler, and therefore less dependable keys. Add to these complexities the fact that the work was not available in English and you may have the explanation why this work of Thonner's was almost unknown in the English speaking world. Davis and Cullen do not even mention Thonner's name. In defence of English speaking botanists it may be added that Thonner's The flowering plants of Africa — an analytical key to the genera of African phanerogams, was a standard reference work in the National Herbarium, Pretoria, and that in the days before Phillips's Genera a copy of this work could be found on the desk of every taxonomist. The work on African flowering plants was, incidentally, translated into English by Thonner himself and it was 'revised' by Rendle. It is obvious that the present work was translated by scientists for whom English is not the home language. But this does not detract from the value of the book. Nouns like sept, and adjectives like apert and contort, however, are not easy to get used to. Geesink and his co-workers admit that the key has not become easier as a result of the many additions they had to make in an attempt to account for the many 'segregated' families and the greatest number possible of curious and aberrant genera. Although some of the major couplets used by Thonner are 'notoriously difficult' they have been retained. We are not told which these couplets are, and we are left wondering whether it would not have been possible to replace them with some less problematic contrasts without major alterations to the key. Do we sense a trace of scholastic sadism in the statement that the complexities of the key 'will force students, as we know from experience, to make a clear and careful analysis and logical interpretation of the various parts of the plant'? On the other hand, and 'despite objections from some learned correspondents', the key makes allowance for misinterpretation of some morphological features, such as bracteoles resembling a calyx.

Now for a brief comparison. Thonner emend. Geesink *et al.* aims at completeness, with special emphasis on the Asian and African tropics, and also includes Gymnosperms. Davis and Cullen restrict themselves to families the northern hemisphere reader is likely to encounter in nature or in gardens, and they exclude Gymnosperms. Both works make use of bracketed or parallel keys. Thonner's mammoth key is presented in one sequence interrupted only occasionally by group headings such as Dicotyledones or Choripetalae. The emendators have added a single-page key to all the major groupings at the beginning. Davis and Cullen start with a key to 14 groups. The families in each of these groups can be identified by means of keys which comprise a maximum of 51 couplets. The keys in both works mention the number of the couplet (in brackets) which has directed the reader to the couplet at hand. In Thonner such mention is only made after a long jump, in Davis and Cullen with every couplet. The indices of both books enable the reader to trace all the places in the keys at which a family keys out. A comparison of the indices therefore gives some insight into the different complexities of the two approaches. A few family names are given here, followed by the number of times they key out, first in Davis and Cullen and then in Thonner: Acanthaceae 1/10, Celastraceae 2/39, Leguminosae (sic, in both works) 8/28, Portulacaceae 5/15, Saxifragaceae 9/57, Verbenaceae 2/19 and Zygophyllaceae 3/17.

It came as no surprise when, during a quick, statistically non-significant test, using typical representatives of their families, Davis and Cullen proved quicker to use in most instances. But after all that has been said about the vastness of Thonner's key, the attentive, observant reader will most probably be surprised how quickly he will come up with the correct family name of an unknown member of the floral kingdom once the features asked for in a couplet have been critically analyzed. The choice between the two contrasts is usually easy to make.

Geesink and his co-workers were unable to establish Thonner's method of compiling keys. Equally the reviewer knows nothing of the procedures used by Davis and Cullen or the Geesink group. One thing appears certain, neither made much, if any, use of a computer. The keys do not talk the language of robots, nor is there a smell of overloaded, smouldering leads about them. But the reviewer must confess to a strong liking for another bit of gadgetry, the visual punch card key, as used successfully hy Hansen and Rahn in their Determination of Angiosperm families (Dansk bot. Ark. 26, 1969). Not being involved in teaching and not having much of a head for complexities, I would like to see the vast number of facts amassed in Thonner worked into a set of punch cards made of thin, tough plastic which can rotate around an axis piercing the left hand upper corner of all cards. The left hand margin of the cards would have to be very wide to allow even cards widely separated in the pack to be brought into direct contact.

But, dreams aside, the work by Davis and Cullen has already proved itself as a most successful text book both in Britain and abroad, and it is certain to go from strength to strength. The new Thonner is bound to become a classic, widely prescribed at universities (at least in the Netherlands), and much thumbed (and thumped?) by students. Some of the less brilliant amongst them may, however, be forgiven if, on occasion, they should jump to the conclusion that all lecturers in botany are hybrids.

O. A. LEISTNER

GENUS *MEDICAGO* (LEGUMINOSAE), A TAXOGENETIC APPROACH by K. A. LESINS & I. LESINS. *The Hague: W. Junk.* 1979. Pp. i–xi, 228. 3 colour plates, 72 figures, full cloth. Price Dutch guilders 100/US $52.65.

The genus *Medicago* is probably known to most readers via the cultivated plant lucerne, *M. sativa* L. Probably less well known is the fact that common lucerne is actually an agricultural hybrid swarm developed from a number of species progenitors, *M. sativa* and *M. falcata* in particular.

This monograph of 56 species is the result of a lifetime study by both authors, spanning over 30 years and 38 scientific papers. They consider their work "as an attempt at taxogenetic systematization of the genus *Medicago*, rather than a strict taxonomic treatment which, as regulated by the International Code of Botanical Nomenclature and applied by herbarium taxonomists, is a rather formal system, to say the least." Although I shall criticize their nomenclatural procedure, I will attempt to do so within an appreciation of their painstaking biosystematic approach: "We consider that hybridization, cytological, chemical and every other available method of establishing similarities and differences among taxa should be a normal procedure in taxonomy."

One is immediately attracted to this book, both by its descriptive and striking cover as well as by the binding and the quality of the paper. A closer look, however, forces one to re-evaluate it. The paper is perhaps too shiny, reverse printing shows through and the quality of the photographs is appalling, the authors' intentions and explanations notwithstanding. But, what has all this to do with a book review?

Book reviews may be of two types, the explanatory-content listing type and the explorative-evaluating type. The majority of book reviews in biology tend to be of the former and contribute little to the critical advance of knowledge. This review will be an attempt at exploration and evaluation.

Binding, paper quality, type face and illustrative material are the first things that attract one to a book and to a large extent are the criteria which will entice one to read on. Once one begins to read, one becomes more critical of the layout, the ease of cross-referencing, of indexing, of the suitability of the drawings and photographs and of the authors' sense of organization. Such impressions further influence, perhaps subtly, one's impressions of the author's work.

My first impressions of this book were positive, both because I am interested in the taxonomy of legumes and because, as a rule, I enjoy the quality of W. Junk's publications. My second impression was negative, because the book is difficult to use (no full index, a key with pollen characters, and fuzzy photographs giving little insight into the wide variation one encounters during identification and because of its ambivalence to formal taxonomic rules).

It was only when I applied myself to this review and to the naming of naturalized material of *Medicago* in South Africa that I became aware of its strengths as well.

While I agree in principle with the taxogenetic (or biosystematic) approach to taxonomy, its general applicability to taxonomy is too time-consuming and costly for it to ever be widely used save to unravel agamic or polyploid complexes. It is in the investigation of the origins of crops and weeds and in the sorting out of natural hybrid swarms that it can be most useful. Although the present account has a detailed prelude as seen in the references, readers interested in such problems should also consult Baum (1977) for a more comprehensive and methodological treatment — of *Avena.*

The authors refer on p.131 to the new species *"M. ignatzii* (Boiss.) Lesins & Lesins in honour of Ignatz Urban". No basionym is cited. Similarly, for their new section *Arboreae* (L.) Lesins & Lesins on the same page. On page 129 they propose a new variety, var. *citrina* in *Medicago papillosa* Boiss., but provide no Latin description and cite no holotype. These few examples of names not validly published, detract considerably from the finished product.

I am sure that distribution maps and some cited specimens, both omitted, would have made the book more useful to non-European readers. The authors clearly must have had this information readily available, both from their own large collections and from their extensive travels. It is the latter which must have given them considerable insight into the variation and delimitation of the species that they dealt with. Out of those travels emerges a story of extinctions and rapidly deteriorating environments, seen strikingly in their colour plate 2; a classic example of the destructive power of goats, this time on the Island of Karpathos.

Finally, out of a number of useful ideas proposed by the authors, I have chosen the following quotation: "A reorganization of taxonomic procedures would involve, along with the herbarium type specimen, the deposition of an amount of viable seed in seed banks".

This book is undeniably useful and will be used far and wide. Authors will have to remember, however, that although they may easily rebel against the current International Code of Botanical Nomenclature they will be judged, like Rafinesque, not by the quality of their work but by the idiosyncrasies of their treatments. The botanical fraternity is fickle and forgets with difficulty. The present authors have escaped narrowly.

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C. H. STIRTON

PELARGONIUMS OF SOUTHERN AFRICA, Vol. 2, by J. J. A. VAN DER WALT and P. J. VORSTER with illustrations by ELAPHIE WARD-HILHORST. *Cape Town: Juta.* 1981. Pp. xvii + 148, 50 plates, 50 line drawings. Price R29,50.

The first volume of Pelargoniums of Southern Africa appeared in 1977. It was so successful that a second edition was published in 1979 and in the same year a German edition appeared followed by a French edition in 1980. The success of the book was hardly surprising. The illustrations by Elaphie Ward-Hilhorst are superb and establish her one of the best artists to grace the South African and probably the world botanical scene. In addition, the text is readable and interesting.

The second volume, which is the second in a series of four volumes on *Pelargonium,* will undoubtedly be as successful as the first: the same high standard of illustration and writing has been maintained. A second author has joined Professor van der Walt, namely Dr Piet Vorster, also of the University of Stellenbosch.

The treatment of each of the 50 species follows the same basic pattern. First of all, the derivation of the specific epithet is provided. Then there is a brief description of the main characters of the species followed by a paragraph explaining its relationships. A brief synopsis, type citation, synonymy, and distribution map precede the full length description, habitat, flowering time, first collection and finally, horticultural information. A delightful column-width pencil drawing of the plant accompanies each write-up.

I could detect only one serious error in the book, ie. serious to the nomenclatural purist, but not to the ordinary botanist or layman — an error that is committed by almost every botanist in the RSA who writes popular or semi-popular books, and that is to refer to the correct name as the valid name. Valid refers only to a valid publication of the name and not to the nomenclatural correctness of the name. Typographical errors are few. On p. 45 the hybrid symbol should have been a multiplication sign and not the letter x of the alphabet.

It is a great pity that in Vol. 2 the authors were obliged to report name changes in eight taxa which appeared in Vol. 1. Surely it is desirable to establish the correct names of all the taxa in *Pelargonium* before starting such a series. It would be dreadful, and a reflection on the authors, who are revising the genus, if further changes had to be reported in Vol. 3.

The book is well presented and the colour reproduction is excellent. I can recommend the book unreservedly to all plant lovers.

D. J. B. KILLICK

TREES OF NATAL by EUGENE MOLL. *Cape Town: University of Cape Town* Eco-lab Trust Fund. 1981. Pp. 567 with numerous line drawings and c. 700 distribution maps. Price R12,00.

A book by Dr Eugene Moll on the trees of Natal is well worth waiting for. There are few, if any, botanists who know the Natal trees as he does. Having visited various forests in Natal like the Hawaan, Dhlinza and Dukuduku Forests in the company of Dr

Moll, I can personally vouch for his vast knowledge of Natal trees. I wonder how many botanists today can identify Natal trees by their slash; Dr Moll certainly can. Not only does Dr Moll know his trees, but he is enthusiastic about them and his enthusiasm is infectious. This book is a distillation of his knowledge of Natal trees, presented in such a way that both the layman and unconverted botanist using the book are likely to become enthusiastic about trees. The cover design by Nicola Moll, aged 9, and the poem by Pippa Moll, aged 10, set the tone for the book.

In the Introduction Dr Moll begins by explaining why he decided to write this book and mentions the problem of having to decide whether to include certain species that are clearly trees, but which are not included in the National Tree List (1972). Dr Moll emphasizes that the basic layout and format of the book have been designed with field use in mind. The format is as follows: distribution map, line drawing of leaf/leaves and sometimes habit, national tree number, scientific name and author, common English, Afrikaans and Zulu names, leaf length in millimetres with the usual length in brackets, height of tree in metres with the usual height in brackets, flowering and fruiting times, habitat and lastly, diagnostic features.

Dr Moll's method of indicating the distribution of each tree species may cause problems for some. To understand the method one must realize that the abundance estimates eg. rare, widespread, uncommon, common etc. apply only to the area in which the species occurs and not to the whole of Natal. For example, according to Dr Moll, *Terminalia sericea* is widespread and common; it is not widespread and common in Natal, but only in a small part of northern Zululand, where it obviously occurs fairly uniformly and commonly throughout the area. *Kiggelaria africana* is designated as uncommon and yet it is found throughout most of Natal; the map shows that *K. africana* occurs throughout most of Natal, but everywhere it is uncommon being restricted to forest margins, scrub forest and rocky outcrops. My ecologist and taxonomist colleagues are not particularly enamoured with the method and say it could be misleading.

A section of the Introduction is devoted to the classification of woody communities. Dr Moll portrays diagramatically the relationships between rainfall, soils, forest, scrub forest and bushveld and then by a series of profile diagrams he distinguishes between the different types of forest and bushveld.

Following the Introduction, are sections dealing with Zulu names and how to use the book. Then there is a simple illustrated key to the ten major groups of trees and interspersed in the text are keys to the groups. I have not used the keys yet, but a colleague of mine, Dr Otto Leistner, has tested them in the Pretoria area and found them to work very well.

The text proper, pages 4–522, describes over 700 species, 2 or 3 species to a page. As already indicated, the information provided for each species is basic and runs to only 5 or 6 lines. Some of the habit sketches, for example of *Cussonia* spp., are delightful crude but nevertheless informative. Arrows point to salient features of each species. I have carefully studied Dr Moll's 'diagnostic features' and found them to be specific and well chosen. He has not missed, for example, the neat, round holes in the leaves of *Scolopia flanaganii,* the waxy covering on the leaves of *S. zeyheri* which is revealed when the leaves are broken, the winged ridges on the twigs of *Syzygium guineense* subsp. *gerrardii* or the fine silver threads which connect the two broken halves of leaves of *Maytenus acuminata.* However, I would like to have seen him mention the sticky glands on the leaves of *Philippia evansii.* In the Drakensberg I initially found it difficult to distinguish between *Philippia evansii* and *Erica ebracteata,* two common heathland shrubs, until I discovered that if I firmly grasped a leafy twig and found it to be sticky, it was *Philippia evansii,* otherwise it was *Erica ebracteata.* Also, in the drawings of the pinnules of *Alsophila capensis* and *A. dregei,* the tree ferns, it would have required very little extra effort to show the position and number of the sori — quite different on the two species and certainly diagnostic.

Typographical errors are few: on pp. 190, 192 and 194 *Scolopia flanagannii* should be *S. flanaganii;* in the index on p. 554 *Trichilia dregeane* should be *T. dregeana* and pendent and scandent are sometimes spelt pendant and scandant respectively.

Trees of Natal is obviously meant to be used in the field, but the cover is hardly suitable for field use. I would have thought that a telephone directory type of cover would have been more servicable and durable than the glossy cover provided.

Dr Moll's new book will undoubtedly be a constant companion on my visits to Natal and, at the reasonable price of R12,00, I can recommend it unreservedly to all those interested in trees.

D. J. B. KILLICK

SEEDLINGS OF DICOTYLEDONS by E. F. DE VOGEL. *Wageningen: Centre for Agricultural Publishing and Documentation.* 1980. Pp. iv & 465, 178 figs, 20 colour plates. Price *f*150 (c. R54,50).

Reviewing this book proved to be an interesting and pleasurable experience. For many years, we have felt the need in South Africa for a book of this nature to assist ecologists, foresters and other botanically orientated workers to recognize seedlings in the field. This book is an excellent example of its kind and could serve as a valuable model for the comprehensive South African study that is needed. In addition, it is of great value as a reference source on a variety of topics, for instance to the work of Bokdam on African Sapotaceae.

Although following in a number of respects the models provided by some earlier workers such as Troup, Duke, de la Mensbruge and Burger, de Vogel has expanded the scope of his treatment to provide surprisingly complete descriptions of the seedlings of the 150 woody Malesian taxa discussed. The approach and scope are very thorough throughout as can be seen from the following abridged outline of section headings (there is no formal division into chapters):

Introduction and acknowledgements
Seedling glossary
Structure, function and variation of the seedling parts
Seedling classification
Malesian woody Dicot genera, with indication of seedling type and seedling literature
Classification of the seedling types
Seedlings and taxonomy
Seedling ecology
The seedling project
Contents and limitations of the descriptive part
References
Descriptions and illustrations
Index

De Vogel recognizes 16 types of Dicot seedlings *viz.* (1) Macaranga type: (2) Sloanea type; (2a) Sloanea subtype and (2b) Palaquium subtype; (3) Sterculia stipulata type; (4) Ternstroemia type; (5) Cyclamen type; (6) Heliciopsis type; (6a) Heliciopsis subtype and (6b) Koordersiodendron subtype; (7) Horsfieldia type; (7a) Horsfieldia subtype and (7b) Pseuduvaria subtype; (8) Blumeodendron type; (9) Rhizophora type; (10) Coscinium type; (11) Endertia type: (11a) Endertia subtype, (11b) Chisocheton subtype and (11c) Streblus subtype; (12) Cynometra ramiflora type; (13) Barringtonia type; (14) Garcinia type; (15) Hodgsonia type; and (16) Orobanche type. These types and subtypes are described and illustrated, followed by a surprisingly comprehensive and well illustrated account of Malesian woody dicotyledonous seedlings. This includes a useful summary of Malesian woody dicot genera with indications of seedling type and seedling literature. The discussion of the classification of seedling types which follows is very interesting, particularly the attempts to unravel evolutionary trends to indicate which are possibly the more primitive states and which are the more advanced. The list of Malesian woody dicot genera and families, with indications of seedling type, includes many genera that also occur in South Africa.

Reviewing non-Malesian literature as well as studying Malesian seedling morphology, de Vogel adduces evidence from all over the world. Some of this makes fascinating reading in its own right apart from its value in developing an argument. For instance, Léonard's comparison of seedlings of *Guibourtia conjugata, G. coleosperma* and *Colophospermum mopane* where reduction of the cotyledons in *Guibourtia* culminates in their seeming disappearance in *Colophospermum.* The hypothesis is sustained that the primitive seedling type is the *Horsfieldia* type with haustorial cotyledons in the endosperm. From this hypothesized primitive type, four pathways of differentiation can be traced along which other seedling types can be arranged.

In the section on seedlings and taxonomy the taxonomic value of certain seedling attributes is discussed. In the following section on seedling ecology, the different types of seeds and varying seed longevity are discussed in terms of environmental conditions of their habitats including such factors as fire. The sections on light sensitivity, germination, establishment and speed of growth, and seedling survival are valuable additions to the text and the insights given add considerably to the practical worth of the book. The description of the seedling project gives useful practical tips should anyone intend undertaking a similar project in South Africa.

The contents and limitations of the descriptive part of the text are described and include explanatory notes concerning the way in which descriptions are set out (to make comparison easy, each part is described in its main stages). There are also notes concerning the illustrations, how they were prepared and so forth. The development of a seedling into a sapling is in most cases adequately documented by three or four illustrations. The first picture shows the mode of germination. Epigeal seedlings in a later stage are depicted with the (para)cotyledons extracted and fully developed, sometimes also with the first few leaves. Hypogeal seedlings in a later stage are illustrated with the shoot partly developed, showing the scale-leaves if present and also some of the developed leaves. The third and fourth pictures show stages of the young sapling usually with a relatively large number of leaves, and often with the (para)cotyledons and some of the lowest leaves already shed. In some cases, it was necessary to provide more illustrations, or details were added, to give additional information.

The results are presented in a logical and practically useful fashion. Genera are arranged alphabetically within families which are in turn arranged alphabetically. Comprehensive literature references are given and also very full statements on the distribution of each genus discussed. The sequence of developments of the parts is described, supplemented by discussion of resting stages and other growth details. General information is given on the germination type and seedling type, followed by a detailed morphological description.

A full list of references consulted is given. There is also a full index to names of plant taxa mentioned in the text (including *Combretum collinum* and *C. zeyheri).*

Descriptions and illustrations are given of 148 taxa. It can be noted in passing that, notwithstanding the title of the book, *Gnetum* is not a dicotyledonous genus. Genera that I noticed also occurring in South Africa (and that would be interesting to compare with the seedlings of South African species) are the following:

Genus	*Family*
Capparis	Capparidaceae
Salacia	Celastraceae
Cuscuta	Convolvulaceae
Diospyros	Ebenaceae
Croton	Euphorbiaceae
Drypetes	Euphorbiaceae
Macaranga	Euphorbiaceae
Scaevola	Goodeniaceae
Garcinia	Guttiferae
Beilschmiedia	Lauraceae
Cryptocarya	Lauraceae
Afzelia	Leguminosae
Desmodium	Leguminosae
Sophora tomentosa	Leguminosae
Barringtonia racemosa	Lecythidaceae
Strychnos	Loganiaceae
Memecylon	Melastomataceae
Orobanche	Orobanchaceae
Ziziphus	Rhamnaceae
Rhizophora	Rhizophoraceae
Parinari	Rosaceae
Prunus	Rosaceae
Canthium	Rubiaceae
Gardenia	Rubiaceae
Pavetta	Rubiaceae
Psychotria	Rubiaceae
Clausena	Rutaceae
Sterculia	Sterculiaceae

Colour plates include illustrations of *Terminalia* and *Barringtonia racemosa.*

Errors are few and far between. As far as I can see, the most glaring have been spotted and are pointed out in the short list of errata. Another slight slip seems to be indicated in the reversed order of Fig. 121 and Fig. 120. Considering that English is not the author's home language, there are very few lapses and these can be easily forgiven. On the whole, this is a very good book and I hope that it will be a trend-setter to stimulate similar work in South Africa.

J. C. SCHEEPERS

CLASSIFICATION AND ORDINATION. ADVANCES IN VEGETATION SCIENCE, 2. ED. E. VAN DER MAAREL. *The Hague: Dr W. Junk* 1980. pp. 198, 100 figs, 12 tables. Price Dfl 145, US$ 76.

As a rule, book reviews do not begin with references to books other than the one being considered. However, as this book can be viewed, in part, as a revision of two earlier volumes, this reviewer is going to break the rule, such as it is. Some four years ago, Whittaker (1978a, 1978b) brought together in excellent fashion the state of the art in classification and ordination in ecology. In the present book, important advances since then in both ordination and classification are described for the first time in the open literature while repeated reference is made to the earlier volumes in the contributions.

M. O. Hill and H. G. Gauch describe DECORANA, an ordination technique which improves upon reciprocal averaging which was shown in 1978 to be 'the best on the market'. It is indeed, as stated by Hill and Gauch, a big step in the right direction towards the ideal ordination technique with which it will be possible to trust almost any data set. H. G. Gauch also describes COMPCLUS, an interactive algorithm for the rapid initial clustering of large data sets. Particular attention was paid to computational efficiency, usually a problem with large data sets, and the procedure described should find favour with ecologists on both computational and ecological grounds. The point is made, however, that COMPCLUS differs fundamentally from hierarchial clustering in that relationships between clusters have to be determined after classification, usually by ordination of composite samples identified by the classification.

The historical development of ordination and classification is described by P. Greig-Smith, a person ideally qualified for the task through his long and intimate association with the subject. This excellent review of the constraints and influences which have affected the development of classification and ordination of vegetation is recommended to all ecologists. He rightly points out that the limitations of real data (as opposed to simulated coenocline 'numbers') suggest that developments of technique are at risk of becoming too concerned with refinements in methodology. He concludes by stating that increasingly complex methods and increasing availability of programs for such methods carry the risk that they may be used without adequate understanding of what they do. This warning cannot be given too often.

M. P. Austin reviews the models of vegetation response to environment which are explicitly or implicitly assumed by current methods of indirect vegetation analysis. These include the Gaussian response model of the Cornell Ecology School, Ellenberg's ecological displacement model and the environmental stress model of Grime. He concludes that progress towards the development of an appropriate model is hampered by the lack of sufficient direct gradient studies; interpreted by the reviewer as a call for further detailed plant-environment relationship studies.

The theoretical/philosophical papers also include contributions by L. Orlóci, I. C. Prentice, E. Feoli, E. van der Maarel, S. Pignatti and others. Papers leaning further towards the practical application of ordination and classification include contributions by S. Jensén, R. S. Clymo, R. K. Peet, O. Wildi, J. Lepart, P. van Hecke and others. A good balance between theory and practice is maintained in the volume.

There is a total of 24 chapters, including the introduction and preface. All the full-length scientific papers have appeared previously in *Vegetatio*. Although most of them were also read at a symposium on 'Advances in vegetation science' held in The Netherlands during 1979, by including some papers prepared after the symposium, an up-to-date volume has been produced. Initially, the duplication of papers in *Vegetatio* and this volume appeared unnecessary but on studying the book at greater depth it was found to be an extremely coherent and valuable contribution, particularly for ecologists who neither subscribe to *Vegetatio* nor have ready access to it. It is a worthy companion and successor to the earlier volumes referred to.

REFERENCES

WHITTAKER, R. H., (ed.), 1978a. *Ordination of plant communities.* The Hague: Dr W. Junk.

WHITTAKER, R. H. (ed.), 1978b. *Classification of plant communities.* The Hague: Dr W. Junk.

J. W. MORRIS

BEKENNTNISSE EINES ÖKOLOGEN. Erlebtes in acht Jahrzehnten und auf Forschungsreisen in allen Erdteilen (Confessions of an Ecologist. Experiences during eight decades and on research tours on all continents) by H. WALTER. *Stuttgart: Gustav Fisher Verlag.* 1980. Pp. 334, 12 figures. Price DM19.00 (R8,60).

Another subtitle of this work could have been "The other side of a botanist's life", and very few botanists would have so much to tell about that other side as Professor Walter. This book is an ideal complement to the scientific work of this well-known scientist, with his 24 books and 166 scientific publications.

The work is chronologically arranged and begins with the youth of the author in Russia, his experiences during the First World War, his graduation in Jena and his first academic appointments. Special highlights of the book are the research trips to different parts of Europe, U.S.A., Africa and America. The experiences and adventures during these tours and expeditions are fluently related, and with its many anecdotes, the book makes for captivating reading from cover to cover.

The reader may have questions such as: 'How did Professor Walter see my country at the time?'; 'Which scientists did he meet?' And to these and other questions Walter provides many informative and interesting answers. A recurrent theme throughout the work is the author's gratefulness to the Almighty for a life full of opportunities and rich in experiences. As botanists, we are thankful to Professor Walter for this book, for his great scientific work and his dedication to botany, which has helped to promote this science all over the world.

With its fluent style and highly informative contents, the book is warmly recommended to anyone wishing to know more about the life and work of Professor H. Walter. An English edition would ensure for this work the wider impact that it deserves.

P. J. WEISSER

HEATHLANDS AND RELATED SHRUBLANDS: ANALYTICAL STUDIES (Ecosystems of the World, Vol. 9B) edited by R. L. SPECHT. *Amsterdam: Elsevier Publishing Company.* 1981. Pp. xvi + 385. 89 figures and numerous tables. Price Dfl. 170/US $83,00.

Descriptive ecological studies are incomplete without attendant analytical ecological process studies. The volume Heathlands and Related Shrublands: Descriptive Studies, appeared in November 1979 and is well known (Review by H. C. Taylor, 1981. Bothalia 13:589-590). The long awaited companion volume, Heathlands and Related Shrublands: Analytical Studies, also edited by R. L. Specht, appeared in February 1981 and represents a significant advance in consolidating knowledge of various processes in heathland ecosystems. The second volume is number 9B in the series, Ecosystems of the World with D. W. Goodhall as editor in chief. Enlisting the services of an international spectrum of 24 researchers and including his own direct involvement in seven of the 26 chapters, Professor Specht has achieved a synthesis of information that was not previously available in one volume. It is to be hoped that a second edition will soon be forthcoming since the mean date of completion of manuscripts was in January 1977. A possible reason for the publishing delay relates to the second volume containing extensive indices — almost a third the number of pages of the volume — covering both volumes 9A and 9B. The delay did have the advantage that certain corrigenda to the first volume could be included at the back of the second.

Chapters are grouped into six sections that are identified only in the table of contents. The first section addresses the topics of seasonal growth, flowering and faunal rhythms. In the first of the four chapters of this section, Kruger summarizes the state of published and some unpublished information on seasonal shoot growth and flowering in South African heathlands. The important point of the overall impression of interspecific asynchrony in fynbos phenology is made. In the following chapter, Specht, Rogers and Hopkins suggest, mainly on the basis of phenological data, that Australian heathlands, south of the Tropic of Capricorn are composed of a mixture of species with different temperature optima. These are in turn related to climatic changes that have occurred since the Tertiary. Edmonds and Specht show how seasonal faunal rhythms in South Australian heathland are generally closely tied to seasonal activity of the plant producers. Welcome attention to mechanisms of seasonal growth and flowering rhythms in European heathlands is provided by Woolhouse and Kwolek. They also make the interesting distinction between visible phenophases (for example, shoot growth) and hidden phenophases (for example, carbohydrate reserves). This chapter reads advantageously in conjunction with the work of Heal and Perkins (1978)* that appeared after submission of this chapter.

The second section deals with pollination and seed dispersal but is limited to Australian heathlands. Most emphasis is placed on the animal vector of diaspores.

The next section deals, in two chapters, with fire tolerance in heathland vegetation and animals. I found the first chapter by Gill and Groves particularly interesting. The well organized and clearly written body of information also includes some reference to fire effects in South African fynbos.

The following six chapters constitute a section on climatic stress. Yates provides a synopsis on the optical properties of heathlands with emphasis on reflectivity of heathland communities. The remaining five chapters of this section concern water relations. These range from: the suppression of plant performance through seasonal waterlogging (Specht); morphological adaptation to waterlogging, mainly in Restionaceae and Cyperaceae (Campbell); physiological effects of waterlogging including adaptations to overcoming oxygen stress (Armstrong); morphological adaptations to drought with emphasis on root systems (Specht) to physiological adaptation to drought (Conner and Doley). The last mentioned authors plead for further work to be undertaken to define adequately the energy and gas-exchange strategies of heathland plants.

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* HEAL, O. W. & PERKINS, D. F. (eds) 1978. *Production ecology of British moors and montane grasslands.* Berlin: Springer-Verlag.

Section five covers nutrient stress in eight chapters. Briefly stated these cover the following topics: the fertility status of heathland soils including consequences of low nutrient status (Groves); nutrient cycling in heathlands with individual treatment of nutrients, mainly phosphorus and calcium (Groves); mycorrhizas and the associated heathland roots (Malajczuk and Lamont); proteoid and dauciform roots with implications of increased uptake efficiencies (Lamont); the role of polyphosphate in the tight phosphorous economy of heathland plants (Coleman and Specht); toxicity to (usually introduced) phosphorous (Ozanne and Specht); the effects of soil acidity and aluminium toxicity where the rôle of exceptionally fine roots inextricably interwoven in the substrate is identified as one of the outstanding problems in plant nutrition in heathland systems (Woolhouse) and the effect of salt spray on the nutrient budgets of exposed coastal heathlands (Parsons).

The last section on conservation tends to differ from much of the rest of the book in applying results from process studies rather than studying the processes themselves. Kruger describes uses of, dangers to, and official management approaches to the fynbos vegetation of South Africa. In Australian heathlands, Specht refers to the phosphorous toxicity effects, discussed earlier in the book, and the potential effects of orange peelings and urinations in forming an imbalance between heath and herbaceous vegetation along tracks. Details on factors controlling infection of the devastatingly important root fungal pathogen, *Phytophthora cinnamomi* are given by Malajczuk and Glenn. It is clear that activities of man are one of the main promoters of this pathogenic threat to heathlands. Conservation in European heathlands is often inseparable from management of heathlands, usually for improved economic gain. As Gimingham describes, such management often involves the 'improvement' of heathlands through replacement or conversion to different types of vegetation. In the few remaining small reserves of lowland heathland, the intrinsic problem of conserving vegetation which owes its origin and maintenance to human intervention, is highlighted.

The book contains a systematic list of genera, an author index, a systematic index and extensive general index. Indices, as stated above, cover both volumes 9A and B. The degree of detail and subject balance is variable as may be expected with such diverse authorship. It is a well produced book with well set out text and many clear figures. Chapters are generally short with a mean length of about nine pages. Although the Australian bias is obvious, this book should serve as a stimulus to the student of heathland ecology in any area. The study field of the functioning of many heathland ecosystems is still wide open, especially with respect to the integration of the effects of functional determinants. A second edition of this strongly recommended book would serve the purpose of updating in the face of the current information explosion and possibly providing opportunity for an integral synthesis of findings.

M. C. RUTHERFORD

THE RADIATION REGIME AND ARCHITECTURE OF PLANT STANDS by J. ROSS. *The Hague: Dr. W. Junk BV Publishers.* 1981. Pp. xxvii + 391, 116 figures and numerous tables. Price Dfl. 220/US$115,00.

A book of great interest to those who aim to understand the functioning of plants, has been largely limited to a Russian readership since 1973. The present translation now readily allows the dissemination of information on the detailed radiation regime of plant stands to the wider English reading scientific community. The volume is one of the first in the series Tasks for Vegetation Sciences which, as Series Editor Professor Lieth of the University of Osnabrück explains, will also be including translations of some other less-available, innovative works.

The author, Dr Juhan Ross, a physicist and founder of the Tartu School of Actinometry, addresses the subject of biophysics of plant parts and assemblages in which he emphasizes the formal development of ideas through mathematical expression. The approach underscores the importance of enlisting the aid of scholars from the physical sciences for formulation of the cohesive body of strictly quantitative theory needed for proper description of plant-environmental interactions.

The book is divided into two parts. The first is the shorter and deals with plant stand architecture, much of which is a prerequisite for the treatment of the radiation regime in plant stands in the second. Following an introduction, in which the relevance of radiation types of plant life is briefly indicated, the author lists the main aims of phytometry. This is valuable to some readers who may otherwise have considered the frequent insertion of the word phytometric in many sentences throughout the book as the aggrandizement of a buzzword. The principle phytometric characteristics of stands are then discussed, considering, in turn, individual plant organs, individual plants and pure stands. The special notation used in formulae to distinguish values pertaining to individual plants from those pertaining to a stand is a practice that could be very usefully employed in some other works. The next chapter on methods commences with those for determining leaf area and here one is led to wonder whether the updating of the book for the translation has allowed for full incorpration of the plethora of available modern planimeters. He proceeds with considering measurement of leaf orientation and discounts for various reasons, inclined point quadrat and stratifying clip methods. Various plant dimension and plant part counts ('statistical methods') are preferred and are integrated into what is termed a "rational method" which allows calculation of, for example, vertical distribution of stand foliage and the distribution function of foliage area orientation for each layer. Intercorrelations between plant dimensions are briefly discussed with more space being allocated to a discourse on the spatial distribution of phytoelements in stands with emphasis on vertical distributions of various leaf attributes. The following chapter is probably one of the most important in the first part and deals with foliage area orientation in stands where the emphasis is not only on angles of inclination and the distribution function of leaf inclination but also the azimuth distribution of foliage. The last chapter of the first part on plant stand architecture, photosynthesis and productivity, appears to stand almost as an afterthought of whether many attributes of stand architecture bare any close relationship to crop yields. Data in this regard appear likely to continue to be controversial until, as the author points out, more prolonged and more comprehensive experiments are undertaken. This chapter may have been more pertinently placed at the end of the book and the question of the relevance of several aspects of the radiation regime in a plant stand to crop yield highlighted at the same time.

In the second part, the author appears to be in his element, that is, the physics of radiation. Basic physics of radiation using fairly simple object models are given in the first two chapters on radiation field and incident radiation. It is interesting that the 400 to 700 nm range for PAR accepted in western countries becomes 380 to 710 nm in Soviet and allied countries. In 'Optical properties of phytoelements' author deals mainly with the scattering phase function in the short-wave region of the spectrum and emission coefficient in the long-wave region. Here plant characteristics are taken into account to a greater extent and include leaf surface roughness, leaf pigments, internal leaf structure and leaf water content. Penetration of direct solar radiation into a plant stand is further considered and includes effects of leaf overlap, vertical distribution of plant material, gap areas and consideration of Nilson's silhouette theory. A somewhat displaced seven page subsection on methods is also found in this chapter. The author proceeds in successive chapters to deal with penetration of diffuse sky radiation into plant stands and the scattering of radiation inside the plant stands. Here the mathematical treatment deepens and becomes consequently, unfortunately daunting to many biologists. The crowning chapter is not reserved for the end; it attempts a synthesis of the total radiation field in plant stands. Assumptions, stand simplifications and special cases are clearly identified. The author admits that the 'proper' calculations here are complex and very laborious and suggests simplifications. These include using a scattering coefficient to avoid integrating over wavelengths and avoiding the issues of multiple scattering and finite depth of the stand. A terse but profound statement concerns the important problem of the relationships between the total radiation field and photosynthesis and yield of stands: 'We will only mention that this is a complicated problem wanting an ultimate solution'. Some other recent models of radiation regime are discussed as well as the application of Monte Carlo simulation models. The second part of the book is concluded by four fairly loose standing but valuable chapters that address practical problems in calculating often used radiation quantities. The first of these chapters deals with simplified empirical models and with the development of semiempirical models of total radiation fluxes which are more practically implimented. This is followed by chapters on the calculation of Albedo, long-wave radiation and net radiation in plant stands. The Book ends with a short conclusion section, a supplement on description of field experiments used, 19 pages of references (many in Russian), an author index and a short subject index.

The book obviously represents a major work and may be considered essential reading for ecophysiologists who, wishing to put the eco into physiology, have long needed to better consider the intricacies of integrating their data over highly variable canopies, stands and communities. It must be remembered, however, that although the book provides a foundation, most of the empirical basis for the theory rests on herbaceous plants such as maize, sunflower and swede. The application to the many canopy architectural models currently identified for tropical trees may be expected to be particularly complex. The physical layout and presentation in the book is neat and pleasing. Figures are usually good with some exceptions, for example, Fig. 42. Some of the usually inevitable gremlins have crept in and we read of, for example, Sunflacks on page 188 and there are one or two literature date discrepancies between text and list. Glib understatements are not common but do include 'In similar way phytometric characteristics of . . . roots are determined'. A nine page list of main symbols used is given at the start of the book which is indespensible for use of the book. As biologists, most of us have seldom absorbed more than a one or two semester course in calculus, with the result that not all the many mathematical derivations are readily appreciated by the wider range of potential users. The author's appeal for interdisciplinary research on the problems of extending radiation distribution theory to more real and varied situations with the working together of mathematicians, physicists, biologists, biochemists and agronomists cannot be too strongly endorsed. This book should find its way on to the shelves of many libraries and the office/laboratories of many ecophysiological researchers.

M. C. RUTHERFORD

SUCCESSION edited by A. VAN DER MAAREL. *The Hague: Dr W. Junk BV Publishers.* 1980. Pp. 151, 106 figures and 26 tables. Price Dfl. 90/US$47,00.

When is the incorporation of a series of separate, already published journal articles into a single book justified? Possibly, when: the articles deal with the same or closely related subject field(s); access to the original articles is difficult; the original articles are placed between extraneous information or are diluted in time; there is a need for a book package to allow for wider individual promotion. Chapters in a book so constituted often have one major advantage over chapters of most books. They are each likely to be served by an abstract or summary. They are, however, most unlikely to cross reference one another and a "selected readings" type volume usually results.

Justification for the separate book entitled Succession may be debatable on some counts since it represents a hard bound copy of the singly issued part of Vegetatio Vol. 43, No 1,2 (1980) with the one page introduction by the editor. The book, however, does have subject unity in consisting of 16 of the succession theme papers presented at a symposium on 'Advances in Vegetation sciences' held at Nijmegen, The Netherlands from 15 to 19 May, 1979. It is volume three in the series, Advances in vegetation science. Almost half the contributors are from Sweden or France with others from, for example, Australia, South Africa and North America.

There are some excellent contributions. One of the most innovative is that by Noble and Slatyer. They suggest a framework where selected 'vital attributes' of plants are used in evaluating the interaction between various species to yield a replacement sequence. This depicts the major shifts in composition and dominance that occur following a disturbance. There are several papers on vegetation succession and diversity in mediterranean climate type areas. In one of these, Campbell and Van der Meulen study alpha and beta diversity relative to vegetation age after fire, and altitude in South African fynbos vegetation. Other papers consider the effects of fire on vegetation stability and relationships between succession and diversity. Interesting results on the drop in the male to female ratios in dioecious plants with succession are presented by Faliński.

Some thought provoking theoretical papers include: that by Fagerström and Agren on possible relationships between phenological spread and stochasticity in plants; Austin's use of divisive information analysis for transition matrix simulation of grassland succession; Glenn-Lewin's questioning of conventional succession theory and the suggestion of an alternative individualistic, independent development; and Van Hulst's investigation of the basis of Markovian vegetation models. Van Hulst concludes that students of vegetational succession should either leave the narrow domain of vegetation dynamics in order to study ecosystem dynamics, or explore different succession models.

By its nature of origin, this volume is neither an introductory text book on succession nor an integrated synthesis on the current state of knowledge of succession theory for the advanced scholar. Rather it provides a cross section of various treatments of succession, many of which, happily, are original and mentally stimulating. Although not all approaches are covered, the book's major value probably lies in stimulating new thoughts in the study of succession. This is needed since parts of classical succession theory have become sterile and need injection of population dynamics theory and the realization that the vegetation elements studied are usually part of a more complete ecosystem that undergoes change.

M. C. RUTHERFORD

GUIDE FOR AUTHORS

GENERAL

Bothalia is a medium for the publication of botanical papers dealing with the flora and vegetation of Southern Africa. Papers submitted for publication in Bothalia should conform to the general style and layout of recent issues of the journal (from Vol. 11 onwards) and may be written in either English or Afrikaans.

TEXT

Manuscripts should be typed, double-spaced on one side of uniformly-sized A4 paper having at least a margin of 3 cm all round. Latin names of plants should be underlined to indicate italics. All other marking of the copy should be left to the editor. Metric units are to be used throughout. Manuscripts should be submitted in duplicate to the Editor, Bothalia, Private Bag X101, Pretoria.

ABSTRACT

A short abstract of 100–200 words in both English and Afrikaans should be provided. In the abstract the names of new species and new combinations should not be underlined.

FIGURES

Black and white drawings, including graphs, should be in jet-black Indian ink preferably on bristol board or plastic film. Lines should be bold enough to stand reduction. Indicate the desired lettering lightly in pencil: the printer will insert the final lettering. If authors prefer to do their own lettering, then use some printing device such as stencilling, letraset, etc. It is recommended that drawings should be twice the size of the final reduction.

Photographs submitted should be of good quality, glossy, sharp and of moderate, but not excessive contrast. Photograph mosaics should be composed by the authors themselves: the component photographs should be mounted neatly on a white card base leaving a narrow gap between each print; number the prints using some printing device.

Figures should be planned to fit, after reduction, into a width of 8 cm, 11 cm or 17 cm with a maximum vertical length of 24 cm.

The number of each figure and the author's name should be written on the back of the figure using a soft pencil.

Captions for figures should be collected together and typed on a separate page headed *Captions for Figures*. A copy of each caption should be attached to the base of each figure.

Authors should indicate in pencil in the text where they would like their illustrations to appear.

TABLES

Tables should be set out on separate sheets and numbered in Arabic numerals.

CITATION OF SPECIMENS

In citing specimens the grid reference system should be used (Technical Note: Gen. 4.). Provinces/countries should be cited in the following order: S.W. Africa, Botswana, Transvaal, Orange Free State, Swaziland, Natal, Lesotho and the Cape. Grid references should be cited in numerical sequence. Locality records for specimens should preferably be given to within a quarter-degree square. Records from the same one-degree square are given in alphabetical order i.e. (–AC) precedes (–AD), etc. Records from the same quarter-degree square are arranged alphabetically according to the collectors' names; the quarter degree references must be repeated for each specimen cited. The following example will explain the procedure:

NATAL.–2731 (Louwsburg): 16 km E. of Nongoma (–DD), *Pelser 354;* near Dwarsrand. (–CB) *Van der Merwe 4789.* 2829 (Harrismith): near Groothoek (–AB), *Smith 234;* Koffiefontein (–AB), *Taylor 720;* Cathedral Peak Forest Station (–CC), *Marriott 74.* Grid ref. unknown: Sterkstroom, *Strydom 12.*

Records from outside Southern Africa should be cited from north to south i.e. preceding those from Southern Africa. The abbreviation 'distr.' should be added to all district names e.g.:

GIDS VIR SKRYWERS

ALGEMEEN

Bothalia is 'n medium vir die publikasie vir plantkundige artikels wat handel oor die flora van Suidelike Afrika. Artikels wat voorgelê word vir publikasie in Bothalia behoort ooreen te stem met die algemene styl en rangskikking van onlangse uitgawes van die tydskrif (vanaf vol. 11). Dit mag in Engels of in Afrikaans geskryf word.

TEKS

Manuskripte moet getik wees in dubbelspasiëring slegs op een kant van ewegroot A4-papier, met reg rondom 'n rand van minstens 3 cm breed. Latynse name van plante moet onderstreep word om aan te dui dat dit kursief gedruk moet word. Alle ander merke moet aan die redakteur oorgelaat word. Metrieke eenhede moet deurgaans gebruik word. Manuskripte moet in tweevoud ingedien word by die Redakteur, Bothalia, Privaatsak X101, Pretoria.

UITTREKSEL

'n Kort uittreksel van 100–200 woorde moet voorsien word, beide in Engels en Afrikaans. In die uittreksel moet die name van nuwe soorte en nuwe kombinasies nie onderstreep word nie.

AFBEELDINGS

Wit en swart tekeninge, insluitende grafieke, moet met pikswart Indiese ink geteken word, verkieslik op 'bristol board' of plastiekfilm. Lyne moet dik genoeg wees om verklein te kan word. Dui die verlangde byskrifte liggies in potlood aan: die drukker sal die uiteindelike byskrifte invoeg. Indien skrywers verkies om hulle eie byskrifte te maak, gebruik dan een of ander hulpmiddel soos letraset of 'n sjabloon. Dit is wenslik dat tekeninge tweemaal so groot as die uiteindelike verkleining sal wees.

Foto's wat ingedien word, moet van 'n hoë kwaliteit wees — glansend, skerp en van matige maar nie oordrewe kontras nie. Fotomosaïeke moet deur die skrywer self saamgestel word: die afsonderlike foto's moet netjies monteer word op 'n stuk wit karton met 'n smal strokie tussen die foto's; nommer die foto's met behulp van een of ander druk-hulpmiddel.

Afbeeldings moet so beplan word dat hulle na verkleining sal pas in 'n breedte van 8 cm, 11 cm of 17 cm met 'n maksimum vertikale lengte van 24 cm.

Die nommer van elke afbeelding sowel as die skrywer se naam moet op die rugkant van die afbeelding geskryf word met 'n sagte potlood.

Onderskrifte vir afbeeldings moet bymekaar getik word op 'n afsonderlike bladsy met die opskrif *Onderskrifte vir Afbeeldings.* 'n Afskrif van elke onderskrif moet aan die onderkant van elke afbeelding vasgeheg word.

Skrywers moet met potlood in die teks aandui waar hulle graag hulle afbeeldings wil hê.

TABELLE

Tabelle moet op afsonderlike velle papier kom en genommer word met Arabiese nommers.

SITERING VAN EKSEMPLARE

Wanneer eksemplare siteer word, moet die ruitverwysing stelsel gebruik word (Tegniese Nota: Gen. 4). Provinsies/lande moet in die volgende volgorde siteer word: Suidwes-Afrika, Botswana, Transvaal, Oranje-Vrystaat, Swaziland, Natal, Lesotho en die Kaapprovinsie. Ruitverwysings moet in numeriese volgorde siteer word. Lokaliteitsrekords vir eksemplare moet verkieslik tot binne kwartgraadvierkante gegee word. Rekords uit dieselfde eengraadvierkant word in alfabetiese volgorde aangebied, nl. (–AC) kom voor (–AD) ens. Rekords uit dieselfde kwartgraadvierkant word alfabeties gerangskik volgens die versamelaars se name, en die kwartgraadverwysings moet herhaal word vir elke eksemplaar wat siteer word. Die volgende voorbeeld sal die metode verduidelik:

NATAL.—2731 (Louwsburg): 16 km O. van Nongoma (–DD), *Pelser 354;* naby Dwarsland (–CB), *Van der Merwe 4789.* 2829 (Harrismith): naby Groothoek (–AB), *Smith 234,* Koffiefontein (–AB), *Taylor 720;* Cathedral Peak Bosboustasie (–CC), *Marriott 74.* Ruitverwysing onbekend: Sterkstroom. *Strydom 12.*

Rekords van buite Suidelike Afrika moet siteer word van noord na suid, d.w.s. dit gaan dié van Suidelike Afrika vooraf.

KENYA.—Nairobi distr.: Nairobi plains beyond race course, *Napier 485.*

REFERENCES

References in the text should be cited as follows: 'Jones (1955) stated . . . ' or '. . . (Smith, 1956)' when giving a reference simply as authority for a statement. The list of references at the end of the article should be arranged alphabetically and the literature abbreviation used should conform to the World List of Scientific Periodicals (1965) or the list of Literature Abbreviations (Technical Note: Tax. 6 AN 1) issued by the Botanical Research Institute, thus:

BROWN, N. E., 1909. Asclepiadaceae. In W. T. Thiselton-Dyer, *Fl. Cap.* 6,2: 518–1036. London: Lovell Reeve.

HUTCHINSON, J., 1946. *A botanist in Southern Africa.* London: Gawthorn.

KRUGER, F. J., 1974. *The physiography and plant communities of the Jakkalsrivier Catchment.* M.Sc. (Forestry) thesis, University of Stellenbosch (unpublished).

MORRIS, J. W., 1969. An ordination of the vegetation of Ntshongweni. Natal. *Bothalia* 10: 89–120.

If, as in many taxonomic papers, periodicals or books are mentioned in the text, usually in the species synopsis, they should be cited as in the following examples: Gilg & Ben. in Bot. Jb. 53: 240 (1915) and Burtt Davy, Fl. Transv. 1: 122 (1926).

REPRINTS

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HUTCHINSON, J. 1946. *A botanist in Southern Africa.* London: Gawthorn.

KRUGER, F.J., 1974. *The physiography and plant communities of the Jakkalsrivier Catchment.* M.Sc. (Bosbou) tesis. Universiteit van Stellenbosch (ongepubliseerd).

MORRIS, J. W., 1969. An ordination of the vegetation of Notshongweni, Natal. *Bothalia* 10: 89–120.

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Bothalia 14, 2: 169–175 (1983)

Southern African species of *Mentha* L. (Lamiaceae)

L. E. CODD*

ABSTRACT

The species of *Mentha* L. occurring in Southern Africa are reviewed and a key is provided to two indigenous and one naturalized species. *M. wissii* Launert is reduced to *M. longifolia* (L.) Huds. subsp. **wissii** (Launert) Codd.

Although *Mentha* is a clearly defined genus, the determination of species limits is not an easy matter and there has been a proliferation of 'species' by certain authors in Europe. The result is that over a thousand specific and infraspecific names have been published, while conservative estimates place the number of good species at between twenty and thirty, most of which occur in the northern hemisphere. Perhaps Walahfrid Strabo was justified when, in the ninth century A.D., he included the following lines in his 'Hortulus' (reproduced, with translation, by the Hunt Botanical Library, 1966):

> 'But if any man can name
> The full list of all the kinds and all the properties
> Of mint, he must be one who knows how many fish
> Swim in the Indian Ocean, how many sparks Vulcan
> Sees fly in the air from the vast furnace in Etna'.

Part of the difficulty in deciding on species limits has been attributed to hybridization. It is also evident that some species are extremely polymorphic, particularly *M. longifolia* (L.) Huds., in which 21 subspecies and 150 varieties were recognized by Briquet. The nomenclature of this species and of the related *M. spicata* L. has also been complicated by Linnaeus adopting a different treatment of the complex in the second edition of his Species Plantarum (1763) from that of the 1753 edition.

In his first edition of 1753, Linnaeus treated members of this complex as three varieties within a single species without indicating a typical variety, as follows:

M. spicata L.
a. var. *viridis* L.
b. var. *longifolia* L.
c. var. *rotundifolia* L.

In edn 2 (1763), he raised the three varieties to species rank, but discarded the name *M. spicata:*

1. *M. viridis* (var. *viridis* L., edn 1)
2. *M. sylvestris* (var. *longifolia* L., edn 1)
3. *M. rotundifolia* (var. *rotundifolia* L., edn 1).

However, in the meantime, Hudson in his Flora Anglica (1762) had dealt with them on the following lines which conform with the modern approach:

1. *M. spicata* (var. *viridis* L., edn 1)
2. *M. longifolia* (L.) Huds.
3. *M. rotundifolia* (L.) Huds.

Unfortunately, most subsequent authors, until recently, have followed the nomenclature put forward in Linnaeus's second edition instead of Hudson's earlier and more logical treatment which should have been adopted.

In the latter part of the same century, J. E. Smith, who had distinguished himself in 1784 by acquiring the Linnaean Herbarium, made a study of British mints and published his conclusions in Trans. Linn. Soc. London 5: 171–217 (1899). One point which affects our flora was his clarification of the distinction between *M. longifolia* and *M. spicata* on the basis of the retrorse-pubescent rhachis and the densely pubescent pedicels and calyx of *M. longifolia* as against the glabrous to sparingly pubescent parts of *M. spicata.*

Although this may serve as a basis for distinguishing between the two species, exceptions may be encountered (Harley 1972, 1972a; Harley & Brighton 1977). Over the greater part of its distribution range in southern Africa, *M. longifolia* (in which three subspecies are recognized) exhibits the characteristically pubescent rhachis and calyx. However, in a small area in the southern Cape Province between Humansdorp and Riversdale, and inland to the Swartberg, specimens have been recorded in which all parts are glabrous but which in general appearance agree with *M. longifolia* rather than with *M. spicata.* The link with *M. longifolia* is further supported by the occurrence of specimens with intermediate grades of pubescence. Cooke in Flora Capensis identified such glabrous specimens (*Burchell* 4798, 6457) as *M. viridis* (a synonym of *M. spicata*) but, with more ample material now available, it is considered that they belong in *M. longifolia* as a form of subsp. *polyadena* and that Cooke's key to the species and subspecies should be modified accordingly. In the present study it is concluded that *M. spicata* does not occur naturally in southern Africa, though it has been found as a recent adventive. It is therefore unlikely that the glabrous and intermediate specimens referred to above have been derived from hybridization between *M. longifolia* and *M. spicata.*

Several species are grown for their essential oils or as culinary herbs, the best known being the Peppermint (*M. x piperita* L.) and the Spearmint (*M. spicata,*), both of which have been tried commercially in South Africa and are discussed by Baarschers, Horn & Rehm (1962). Several species are used medicinally, as is the case with the two indigenous species, *M. longifolia* and *M. aquatica.* The common mint, *M. spicata,* is widely grown for mint sauce and has been found as a garden escape here and there.

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KEY TO SPECIES AND SUBSPECIES IN SOUTHERN AFRICA.

Leaves sessile or subsessile; inflorescence cylindrical, tapering, 10–14 mm in diameter:
Rhachis, pedicels and calyx pubescent:
Leaves linear, 2–4 mm broad .... 1a. *M. longifolia* subsp. *wissii*
Leaves linear-lanceolate to lanceolate or oblong-lanceolate, more than 5 mm broad:
Leaves variously pubescent on one or both surfaces .... 1b. *M. longifolia* subsp. *capensis*
Leaves glabrous or with a few scattered hairs beneath........................ 1c. *M. longifolia* subsp. *polyadena*
Rhachis, pedicels and calyx glabrous, though calyx teeth may be ciliate:
Leaves lanceolate, acuminate, margins shortly and often obscurely toothed. 1c. *M. longifolia* subsp. *polyadena*
Leaves oblong to ovate-elliptic, acute to obtuse, margin serrate; calyx teeth often ciliate ....2. *M. spicata*
Leaves usually petiolate; inflorescence of oblong or globose flower clusters, 14–20 mm in diameter..3. *M. aquatica*

1. **Mentha longifolia** *(L.) Huds.*, Fl. Angl. ed. 1: 221 (1762); Briq. in Natürl. Pfl.Fam. 4,3a: 321 (1896). Cooke in Fl. Cap. 5,1: 304 (1910). Type: from Europe.

M. spicata var. *longifolia* L., Sp. Pl. 576 (1753). *M. sylvestris* L., Sp. Pl. ed. 2,2: 804 (1763); Smith in Trans. Linn. Soc. Lond. 5: 179 (1800); Bak. in Fl. Trop. Afr. 5: 451 (1900), nom. illegit. Type: as above.

Perennial rhizomatous herb; stems erect to straggling, up to 1,5 (–2) m long, usually retrorse-tomentose, rarely (southern Cape) glabrous or subglabrous. *Leaves* sessile to shortly petiolate; in southern Africa linear to linear-lanceolate, lanceolate or lanceolate-oblong, glabrous to finely felted or coarsely pubescent or white-tomentose beneath (see subspecies), freely gland-dotted, apex acuminate, base obtuse to truncate, margin entire to shortly and distantly toothed. *Inflorescence* cylindrical, tapering at the apex, 30–100 × 10–12 (–14) mm, usually of many verticils, often somewhat lax below, dense above; rhachis usually densely retrorse-tomentose, rarely subglabrous or glabrous; bracts reduced, bracteoles linear; pedicels usually hispid. *Calyx* tubular-campanulate, 2–2,5 mm long, densely to sparingly glandular hispid, rarely glabrous (southern Cape). *Corolla* white to mauve, 3–5 mm long. *Stamens* exserted or occasionally abortive.

An extremely polymorphic species, widespread in Europe and the Mediterranean region to eastern Asia, the Canary Islands and extending to Ethiopia and Kenya from where there is a gap to Zimbabwe and southern Africa, where 3 subspecies are recognized (see Key). Known in England as Horse Mint because the leaves are usually unpleasantly scented.

If the South African material were studied in isolation it is probable that separate species status would be accorded to subsp. *capensis* and subsp. *polyadena*, with subsp. *wissii* placed as a subspecies of *M. capensis*. Although subsp. *capensis* and subsp. *polyadena* overlap in Lesotho and in parts of the southern Cape, there are few specimens which can be regarded as intermediate between them. However, seen in perspective, they are obviously extensions of the *M. longifolia* complex. In the northern hemisphere the leaves of this species may be ovate to ovate-oblong or oblong-lanceolate, but in southern Africa the leaves tend to be narrower in relation to the length, being lanceolate-oblong to linear-lanceolate or linear (subsp. *wissii*). In this region, subsp. *polyadena*, with glabrous leaves, is probably one of the most clear-cut subdivisions of the species. In subsp. *capensis* the leaves vary a good deal in the degree of pubescence and the subject is discussed more fully under the subspecies. For obvious reasons synonymy has been limited to names applicable in southern Africa.

(a) subsp. **wissii** *(Launert) Codd,* stat. nov.

Mentha wissii Launert in Mitt. bot. StSamml., Münch. 2: 311 (1957); Launert & Schreiber in Prodr. Fl. S.W. Afr. 123: 19 (1969). Type: S.W.A./Namibia, Brandberg, *Wiss* 1418 (FR, holo.; M; PRE!).

Leaves linear, grey-green, finely felted on both surfaces, 25–70 × 1,5–4 mm, margin entire or obscurely and distantly toothed.

Recorded from two localities in South West Africa/Namibia (the Brandberg and Naukluft) and from near Garies in Namaqualand; in watercourses and moist places. The leaves are said to be strongly and unpleasantly aromatic.

S.W.A.—2114 (Uis): Brandberg, Numas R. (–AA) *Wiss 1418; 1440.* 2416 (Maltahöhe): Naukluft (–AB), *Dinter 8288*; *Strey 2008*; *Giess 3879*; *8249*; *Tölken & Hardy 675; Merxmüller & Giess 28155; Müller & Tilson 882.*

CAPE.—3018 (Kamiesberg); Kamiesberg (–AC), *Ecklon s.n.* (SAM); near Garies (–CA), *Pearson 5265* (SAM); *5641.*

This group of specimens is very closely allied to subsp. *capensis* and is separated only on the grounds of the rather distinctive linear leaves. The pubescence of the leaves and the inflorescence characters are in no way different from subsp. *capensis*. One or two specimens from Namaqualand have linear-lanceolate leaves and are therefore intermediate between subsp. *wissii* and subsp. *capensis*. In addition, Dr Harley (personal communication) has informed me that, in cultivation, subsp. *wissii* sometimes produces broader leaves than usual, suggesting that separate status for subsp. *wissii* can scarcely be supported. However, the plants from the wild state with linear leaves can be recognized without difficulty and, because they occupy a separate geographical area, it is considered that subspecies status is appropriate in the present state of our knowledge.

(b) subsp. **capensis** *(Thunb.) Briq.* in Natürl. Pfl.Fam. 4,3a: 321 (1896); Cooke in Fl. Cap. 5,1: 304 (1910); Phillips in Ann. S. Afr. Mus. 16: 242 (1918); Wilman, Checklist Griq. West 228 (1946);

Jacot Guill., Fl. Lesotho 239 (1971); Ross, Fl. Natal 304 (1972). Type: Cape, Lions Head, *Thunberg* s.n. (UPS).

M. capensis Thunb., Prodr. 95 (1800); Fl. Cap. ed. Schult. 444 (1823); Briq. in Bull. Soc. bot. Genève 5: (1889). *M. longifolia* var. *capensis* (Thunb.) Briq. in Bull. Herb. Boiss. 4: 687 (1896).

M. salicina Burch. ex Benth., Lab. 170 (1833); in DC., Prodr. 12: 168 (1848). *M. longifolia* subsp. *capensis* var. *salicina* (Burch. ex Benth.) Briq. in Natürl. Pfl.Fam. 4,3a: 321 (1896); Cooke, l.c. 304 (1910). Type: Cape, Roggeveld, Riet River, *Burchell* 1372 (K, holo.!).

M. lavandulacea sensu Benth. in E. Mey., Comm. 232 (1837); in DC., Prodr. 12: 165 (1848), partly.

—var. *latifolia* Benth. in DC., Prodr. 12: 165 (1848). Syntypes: Cape, Cafraria, Witbergen, *Ecklon* s.n.; *Drège* s.n. (K!); *Burchell* 2645 (K!).

M. capensis subsp. *bouvieri* Briq. in Bull. Soc. bot. Genève 5: 76 (1889). *M. longifolia* var. *bouvieri* (Briq.) Briq. in Bull. Herb. Boissier 4: 687 (1896). *M. longifolia* subsp. *bouvieri* (Briq.) Briq. in Natürl. Pfl.Fam. 4,3a: 321 (1896). Type: Cape (Uitenhage, Coega River), *Ecklon & Zeyher* 673 (in. Hb. Delessert, G, holo.; SAM!). This specimen was cited, without locality, in Bull. Herb. Boissier 4: 687 (1896). The locality was obtained from the specimen in SAM.

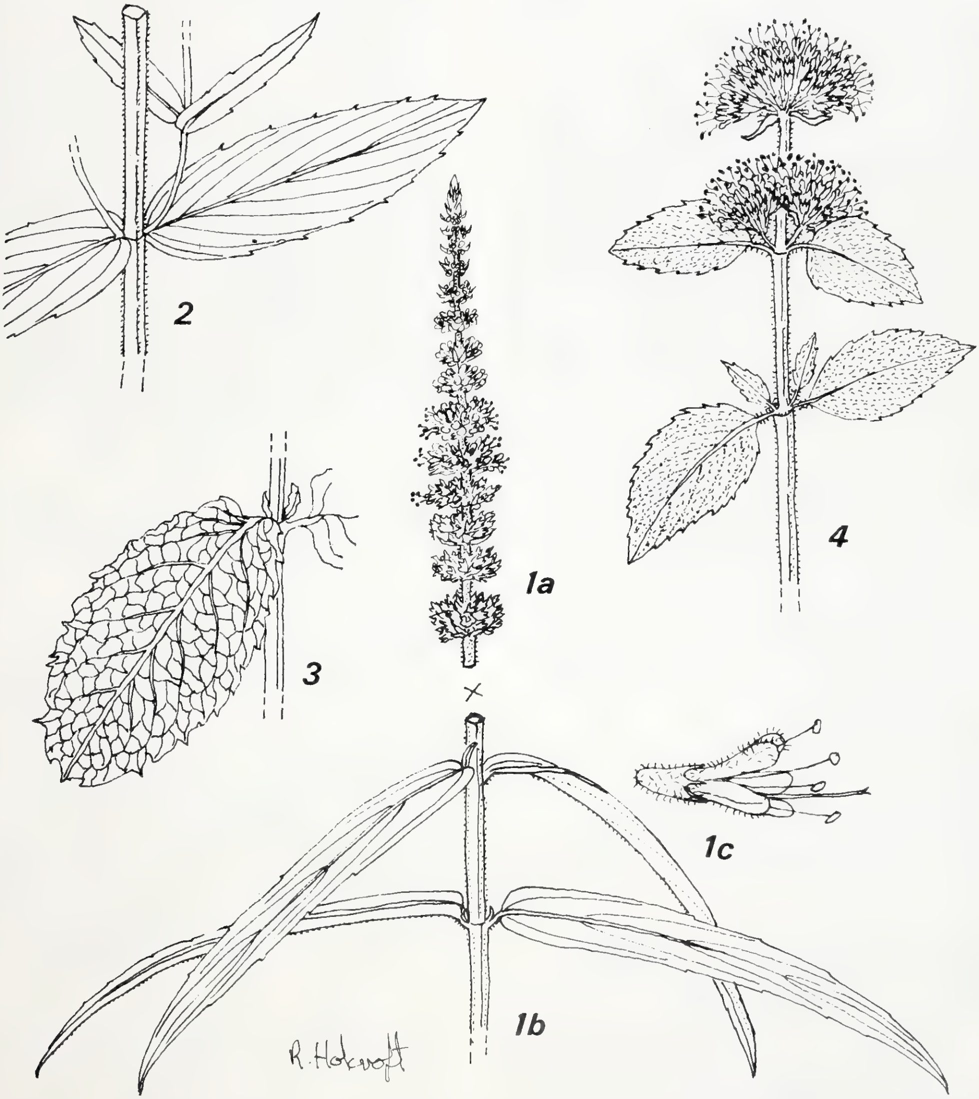
M. longifolia var. *obscuriceps* Briq. in Bull. Herb. Boissier 2: 695 (1894); Cooke, l.c. 304 (1910). Type: without collector or locality, in Herb. Delessert (G, holo.).

—var. *doratophylla* Briq., l.c. 695 (1894); Cooke, l.c. 305 (1910). Type: Cape, *Mund & Maire* (B).

—subsp. *capensis* var. *cooperi* Briq. ex Cooke, l.c., 304 (1910). Type: Cape, Fort Beaufort district, *Cooper* 555 (K, holo.!).

M. longifolia sensu Salter in Fl. Cape Penins. 695 (1950); sensu Jacot Guill., l.c. 239 (1971).

Leaves sparingly to finely pubescent and greyish to dark coloured above, densely white-tomentose to thinly greyish pubescent beneath, lanceolate to linear-lanceolate, (30−) 45−90 (−100) × (5−) 7−18 (−22) mm, apex acuminate, base obtuse to truncate, margin entire to shortly and distantly toothed. (Fig. 1a, b, c.)



FIGS 1−4.—1, *Mentha longifolia* subsp. *capensis;* 1a, inflorescence, × 1; 1b, leaves, × 1; 1c, flower, × 5 (plant from Kirstenbosch seed). 2, *M. longifolia* subsp. *polyadena,* × *1(Pont* s.n.) 3, *M. spicata,* × 1 (cultivated plant). 4, *M. aquatica,* × 1 (*Breyer* sub TRV 19520).

A fair amount of variation in leaf pubescence is included in the above concept of subsp. *capensis.* The typical form, with leaves white-tomentose beneath and greyish to dark-coloured above, includes the types of *M. salicina* Burch. ex Benth., subsp. *obscuriceps* Briq., subsp. *doratophylla* Briq., var. *latifolia* Benth. and var. *cooperi* Briq. ex Cooke. This form is distributed from the Orange Free State and adjacent parts of the south-western Transvaal, northern Cape and Lesotho to the eastern Cape and to the Peninsula, extending northwards to the Calvinia District.

Specimens are now included in subsp. *capensis* from north of this distribution area, e.g. from western Transvaal (*Thode* A1488, *Leendertz* sub TRV 11518), northern South West Africa/Namibia (*Leistner* et al. 143) and from Zimbabwe, which have concolorous grey-green leaves, finely pubescent above and thinly to coarsely pubescent beneath. Specimens with leaves having similar pubescence are found sporadically further south, e.g. *Pearson* 1553 and *Compton* 8512 from the Laingsburg area, and *Pappe* s.n. from Devils Peak. A specimen with pubescence of this kind (*Ecklon & Zeyher* 673 from Uitenhage area) was described as subsp. *bouvieri* Briq. In fact, further study is desirable of the extent to which the present concept of subsp. *capensis* grades into *M. longifolia* subsp. *schimperi* (Briq.) Briq. of Ethiopia and other forms of *M. longifolia* from the northern hemisphere.

Subsp. *capensis* appears to be absent from an area in the southern Cape between Humansdorp and Riversdale and, inland, to the Swartberg, in which area it is replaced by a form of subsp. *polyadena.* Along the margins of this area there appears to be some introgression between the two subspecies. Examples of specimens which have dark green concolorous leaves like subsp. *polyadena* but with the leaf surface puberulous to sparingly pubescent, especially on the nerves beneath are: *Lewis* 4222 and *Barker* 7883 from the Humansdorp area, and *Burchell* 7196 from near Riversdale. These specimens are all included in subsp. *polyadena* but an intermediate specimen with more strongly developed pubescence, *Goldblatt* 1686 from near Montagu, is included in subsp. *capensis.* On the other hand, both subspecies occur in Lesotho with no evidence of intermediates occurring.

ZIMBABWE.—1731, Harare district: *Eyles 1929; Phipps 2493; Biegel 5189.*

S.W.A./NAMIBIA.—1712 (Posto Velho); Kaokoveld, Otjomborombongo (−BB), *Leistner et al. 143.*

TRANSVAAL.—2526 (Zeerust); Zeerust (−CA), *Thode A1488; Leendertz sub TRV11518.* 2725 (Bloemhof): S.A. Lombard Nature Reserve (−DA), *Leistner 113.*

O.F.S.—2828 (Bethlehem): Bethlehem (−AB), *Potts 2993; Roberts 3307;* farm Koeberg (−CB), *Scheepers 1858;* Golden Gate National Park (−DA), *Liebenberg 6853.* 2924 (Hopetown): Riet River Station (−BA), *C. A. Smith 5183.* 2925 (Jagersfontein): Fauresmith (−CB); *C. A. Smith 5240.*

LESOTHO.—2828 (Bethlehem): Leribe (−CC), *Dieterlen 214;* Khabos (−CD), *Fawkes 269* (NBG). 2927 (Maseru): Makhaleng (−AB), *Ruch 1603; 1604;* Mahlatsa (−BB), *Jacot Guillarmod 457;* Roma (−BC), *Schmitz 308;* Maseru (−BD), *Schmitz* 661. 2928 (Marakabei): Molimo Nthuze (−AA), *Schmitz 7230;* Meniameng River (−AA), *Coetzee 474;* Bokong store (−AC), *Jacot Guillarmod 161;* Blue Mtn Pass (−AC), *Bayliss 2624.* 2929 (Underberg): Mokhotlong (−AC), *Compton 21530; Jacot Guillarmod 1106; Liebenberg 5782;* Sehlabathebe Nat. Park (−CC), *Hoener 2209.* 3028 (Matatiele): Qachas Nek (−BA), *Beverley & Hoener 551.*

CAPE.—2823 (Griekwastad): Ongeluk (−CA), *Burchell* 2645 (K); Campbell (−DC), *Wilman sub KMG 23501.* 2824 (Kimberley): Riet River (−CD), *Acocks H1138.* 2922 (Prieska): Orange River, near Prieska (−DA), *Bryant 1055.* 3026 (Aliwal North): Aliwal North (−DA), *Flanagan 1519.* 3027 (Lady Grey): Witteberg (−CD?), *Drège 4766a* (K). 3028 (Matatiele): Naudes Nek (−CA), *Hutchinson & Dyer 3130; Hilliard & Burtt 3775.* 3029 (Kokstad): Kokstad (−CB), *Mogg 4834.* 3118 (Vanrhynsdorp): Heerenlogement (−DC), *Pole Evans & Van Nouhuys 56.* 3119 (Calvinia): (−BD), *Adamson D108; C. A. Smith 2467.* 3123 (Victoria West): Murraysburg (−DD), *Thorne s.n.* 3124 (Hanover): Roelofsfontein (−DA), *Hanekom 2073.* 3125 (Steynsburg): Middelburg (−AC), *Verdoorn 1566; Gill 44; Watt & Brandwyk 1941; Theron 116;* 3126 (Queenstown): Jamestown (−BB), *Barker 2153* (NBG). 3128 (Umtata): Tsitsa River (−BA), *Schlechter 6372.* 3219 (Wuppertal): Baliesgat (−CB), *Hanekom 1378.* 3220 (Sutherland): Great Riet River (−BB), *Burchell 1372* (K); Verlaten Kloof (−DA), *Hall 977* (NBG). 3221 (Merweville): Fraserburg district, Rietvlei River (−AB), *Shearing 17.* 3222 (Beaufort West): Beaufort West (−BD), *Gibbs Russell et al. 203.* 3225 (Somerset East): Bergkwagga Park (−AD), *Brynard 71; Muller 617;* Somerset East (−DA), *Brown s.n.* 3226 (Fort Beaufort): *Cooper 555* (K); Shiloh (−BB), *Baur 53* (K); Alice (−DD), *Acocks 9816; Giffen 1425; 1554.* 3227 (Stutterheim): Debe Nek (−CC), *Batten 6/113* (NBG); King Williams's Town (−CD), *Sim s.n.;* Komga (−DB), *Flanagan 424.* 3228 (Butterworth): Kentani (−CB), *Pegler 1157.* 3318 (Cape Town): Devils Mt (−CD), *Ecklon & Zeyher s.n.* (SAM); *Pappe s.n.* (SAM); Lions Head (−CD), *Wolley Dod 2337.* 3319 (Worcester): Prince Alfred (−AD), *Schlechter 9985;* Muishond River (−AD), *Esterhuysen 1802;* Robertson (−DD), *Britten 639.* 3320 (Montagu): Matjesfontein (−BA), *Pearson* 1553; Whitehill (−BA), *Compton 8512* (NBG); *13171* (NBG); Montagu (−CC), *Goldblatt 1686.* 3325 (Port Elizabeth): near Enon (−BC), *Drège 4766c* (K); Winterhoeksberg (−CB), *Ecklon & Zeyher s.n.;* Coega River, *Ecklon & Zeyher 673* (SAM). 3326 (Grahamstown): Alicedale (−AC), *Brink 109;* Grahamstown (−BC), *Bowker s.n.;* Alexandria (−CB), *Archibald 4938.* 3327 (Peddie): Kidds Beach (−BA), *L. E. Taylor* 5586 (NBG). 3418 (Simonstown): Somerset West (−BB), *Parker 3780* (NBG). 3419 (Caledon): Caldedon (−AB), *Rogers 17548.*

Commonly known in the Karoo and Namaqualand as Balderjan or variations of it, such as Ballerja, Balterja etc. It is also referred to as Wild Mint or Kruisement (Kruistemunt) from the Dutch name for *M. spicata.* The leaves are variously described as having a strong mint-like odour or as smelling of peppermint and are frequently used as a tea to relieve colds and fevers. For this purpose the leaves may be boiled with a little water and sugar until a syrup is formed, of which a tablespoonful is taken three times a day (*Hanekom* 1378).

In Lesotho the vernacular name for both subsp. *capensis* and subsp. *polyadena* is 'koena', a crocodile, reputedly because the plants occur in wet places. Another reason could be that the lanceolate, tapering leaves with small teeth are reminiscent of the shape of the reptile as seen from above. In addition to an infusion being taken as a cure for colds, fresh plants are put under the bedding of a patient in the belief that this will help him to breathe more easily.

(c) subsp. **polyadena** *(Briq.) Briq.* in Natürl. Pfl.Fam. 4,3a: 321 (1896); Cooke in Fl. Cap. 5,1: 303 (1910); Philips in Ann. S. Afr. Mus. 16: 241 (1918); Jacot Guill., Fl. Lesotho 239 (1971). Type: Transvaal, *Otto Lincke* (G).

M. sylvestris L. subsp. *polyadena* Briq. in Bull. Soc. bot. Genève 5: 84 (1889). Type: as above.

M. viridis sensu Benth. in DC., Prodr. 12: 168 (1848), partly, as to *Burchell* 4798 (sphalm 4718), 7196; sensu Cooke, l.c. 305 (1910).

Leaves glabrous on both surfaces or with a few scattered hairs, lanceolate to elliptic-lanceolate or oblong-lanceolate, 35–80 × 8–18 mm, apex acuminate, base obtuse to truncate, margin usually shortly toothed, occasionally subentire. *Rhachis* usually retrorse-tomentose, occasionally glabrous — see note below. (Fig. 2.)

Recorded from two disjunct areas: (a) from the Transvaal, Swaziland, northern Natal, eastern Orange Free State and northern Lesotho; and (b) from the southern Cape Province between the Humansdorp and Riversdale districts and inland to the Swartberg (Fig. 5). Found along watercourses, on river banks and in moist places.

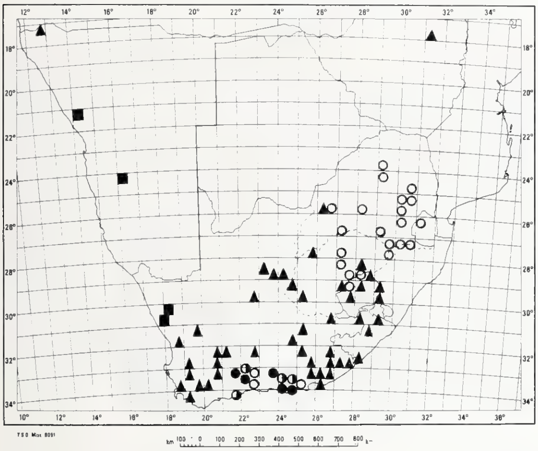


FIG. 5.— ■, *Mentha longifolia* subsp. *wissii;* ▲, *M. longifolia* subsp. *capensis;* ○, *M. longifolia* subsp. *polyadena* (typical); ●, *M. longifolia* subsp. *polyadena* (glabrous rhachis); ◑, *M. longifolia* subsp. *polyadena* (sparingly pubescent rhachis).

The specimens from area (a) are relatively uniform with the rhachis retrorse-tomentose and the calyx densely glandular-pubescent. In area (b), on the other hand, there is a good deal of variation in the degree of pubescence of the rhachis. Some specimens are typical (*Oliver* 5661), some are sparsely pubescent (*Muir* 1973, 2004, *Dahlstrand* 3506), whereas others are completely glabrous (*Acocks* 18189, *Fourcade* 3235). In all the specimens from area (b) the leaf shape is lanceolate to oblong-lanceolate, acuminate, and the general appearance is so similar to the rest of the complex that it would be illogical to separate the glabrous specimens from subsp. *polyadena,* as was done by Cooke in Flora Capensis.

In *M. spicata* (= *M. viridis*), the rhachis and calyx are glabrous but the South African records of this species, which are considered to be garden escapes, have ovate-oblong leaves with serrate margins and can usually be readily distinguished from the glabrous specimens of *M. longifolia* subsp. *polyadena.*

It is interesting that subsp. *capensis,* which is common in the rest of the Cape Province, appears to be absent from area (b). The two subspecies meet in the Humansdorp, Riversdale, Montagu and Swartberg areas and the evidence of introgression between the two is discussed under subsp. *capensis.* As noted previously, the two occur together in Lesotho, but no intermediates from this area have been encountered.

TRANSVAAL.—2329 (Pietersburg): Marabastad (–CD), *Schlechter 4682.* 2429 (Zebediela): Potgietersrus (–AA), *Leendertz sub TRV6553.* 2430 (Pilgrims Rest): Ohrigstad Nature Reserve (–DC), *Jacobsen 2637.* 2526 (Zeerust): Swartruggens (–DA), *Sutton 965.* 2527 (Rustenburg): Crocodile River (–DB?), *Burke 161* (K). 2528 (Pretoria): Aapies River (–CA), *Burtt Davy 1077;* Pyramids (–CA), *Mogg 16768;* Prinshof (–CA), *C. A. Smith 1464;* Pretoria (–CA), *Leendertz sub TRV8561;* Pienaars River (–CB), *Nelson sub TRV11556;* Groenkloof (–CC), *Turner sub PRE10014;* Wolwekloof (–CC), *Mogg 15890;* Fountains Valley (–CC), *Repton 768.* 2530 (Lydenburg): Lydenburg (–AB), *Wilms sub TRV15888;* Dullstroom (–AC), *Galpin 13078;* Rosehaugh (–BD), *Mogg 13679;* Waterval Onder (–CB), *Jenkins sub TRV6706;* Waterval Boven (–CB), *Britten 4733;* Machadodorp (–CB), *Young 26642; Codd 8262.* 2627 (Potchefstroom): Klipdrif (–CB), *Theron 1200.* 2629 (Bethal): Standerton (–CD), *Leendertz sub TRV11015;* near Amersfoort (–DD), *Burtt Davy 4010* (SAM). 2630 (Carolina): Carolina (–AA), *Nicholson H4608.* 2729 (Volksrust): Volksrust (–BD), *Jenkins sub TRV9309.* 2730 (Vryheid): Wakkerstroom (–AC), *Van Dam sub TRV24331; Beeton 129* (SAM); Piet Retief (–BB), *Sidey 1976.*

O.F.S.—2727 (Kroonstad): Kroonstad (–CA), *Pont s.n.* 2827 (Senekal): Willem Pretorius Game Reserve (–AC), *Leistner 3019;* near Ficksburg (–DD), *Jarman 132.* 2828 (Bethlehem): Bethlehem (–CA), *Le Roux s.n.* (NBG); Witsieshoek (–DB), *Junod sub TRV17320.*

SWAZILAND.—2631 (Mbabane): Mbabane (–AC), *Compton 25764; 31162* (NBG).

NATAL.—2729 (Volksrust): Boscobello (–DB), *Jenkins sub TRV12472.*

LESOTHO.—2828 (Bethlehem): Leribe (–CC), *Dieterlen 118; Lubke 219.* 2927 (Maseru): Roma (–BC), *Schmitz 4517; 6588.*

CAPE.—3321 (Ladismith): Gamkaskloof (–BC), *Van Daalen 124* (glabrous). 3322 (Oudtshoorn): Swartberg Pass (–AC), *Marloth 12723* (glabrous); Boomplaas, Cango Valley (–AC), *Hugo 29* (intermediate); Meiringspoort (–BC), *Acocks 18289* (glabrous); Swartberg, east of Blesberg (–BC), *Oliver 5661* (typical); Farm Drinkrivier (–DA), *Dahlstrand 3506* (typical); Kammanassie Mt (–DA/DB), *Rycroft 1900* (NBG, glabrous). 3323 (Willowmore): Baviaanskloof (BC/BD), *Bayliss 3818* (NBG, glabrous). 3324 (Steytlerville): between Cambria and Smitskraal (–CB); *McMurty 1244* (intermediate); Kouga River (–CC), *Fourcade 3235* (glabrous); between Melk River and Gamtoos River (–DD), *Burchell 4798* (glabrous); between Patentie and Mistkraal (–DD), *Lewis* 4222 (SAM, intermediate). 3325 (Port Elizabeth): Gamtoos River (–CC), *Barker* 7883 (NBG, intermediate). 3421 (Riversdale): near Krombek River (–AA), *Burchell* 7196 (K, intermediate); Gourits River, *Burchell* 6457 (K, glabrous); Gourits River mouth (–BD), *Muir* 2004 (intermediate). Grid unknown: Zeekoesdrif, *Muir* 1973 (intermediate).

The qualifying notes relating to pubescence after the Cape specimens refer to the pubescence of the rhachis and calyx.

The plant is used medicinally in the same way as subsp. *capensis.*

2. **Mentha spicata** *L.*, Sp. Pl. 576 (1753); Huds., Fl. Angl. 221 (1762); Bailey, Cyclop. Hort. ed. 21,2: 2035 (1962); Harley in Fl. Europ. 3: 186 (1972). Type: from Europe, in Herb. Hort. Cliff. (BM).

M. spicata var. *viridis* L., Sp. Pl. 576 (1753). *M. viridis* (L.) L., Sp. Pl. ed. 2: 804 (1763); Smith in Trans. Linn. Soc. Lond. 5: 185 (1800); Benth., Lab. 173 (1833); in DC., Prodr. 12: 168 (1848), excl. *Burchell* 4718, 7196; Wilman, Checklist Griq. West 228 (1946); Salter in Fl. Cape Penins. 695 (1950). Type: as above.

Perennial rhizomatous herb; stems ascending up to 600 mm tall, glabrous to sparingly pubescent. *Leaves* sessile to shortly petiolate; blade glabrous or nearly so, somewhat rugose, freely gland-dotted on both surfaces, lanceolate-oblong to ovate-oblong or ovate, 30−50 (−60) × 13−20 mm, apex acute, base obtuse to truncate, margin serrate. *Inflorescence* cylindrical, 30−60 × 10−14 mm; rhachis and pedicels glabrous; bracts reduced, bracteoles linear, glabrous. *Calyx* tubular-campanulate, 2−2,5 mm long, glabrous; teeth sometimes ciliate. *Corolla* mauve to whitish, 4 mm long. (Fig. 3.)

Commonly known as Spearmint, this is the most widely grown species in kitchen gardens for mint sauce etc, and is also cultivated commercially for its essential oil, which is used medicinally and in confectionery. Its origin is lost in antiquity, having probably arisen in cultivation in Europe in ancient times. Its chromosome complement (usually 2n = 48) suggests that it is an allopolyploid, possibly derived from *M. suaveolens* Ehrh. and *M. longifolia* (L) Huds., both of which normally have 2n = 24 (Harley, l.c.). It exists in a wide range of forms, the more desirable ones being propagated vegetatively, and the species is now widely naturalized throughout the world. In South Africa it has been recorded as a garden escape here and there, in moist places.

O.F.S.—2727 (Kroonstad): Heilbron (−BD), *Goossens 510.*

CAPE.—3423 (Knysna): (−AA), *Kapp 93.*

CULTIVATED.—Transvaal: Ermelo district, *Shand s.n.* Cape: Cape Town, *Marloth 7328;* Somerset East, *Brown s.n.;* Grahamstown; *Brink 62.*

As pointed out under the previous heading, certain Burchell specimens identified as *M. viridis* by Bentham in DC., Prodr. 12: 168 (1848) and Cooke in Fl. Cap. 5,1: 305 (1910) are now considered to be a glabrous form of *M. longifolia* subsp. *polyadena.*

3. **Mentha aquatica** *L.*, Sp. Pl. 576 (1753); Thunb., Fl. Cap. ed. Schult. 444 (1823); Benth., Lab. 176 (1833); in E. Mey., Comm. 232 (1837); in DC., Prodr. 12: 170 (1848); Briquet in Natürl. Pfl.Fam. 4,3a: 320 (1896); Cooke in Fl. Cap. 5,1: 305 (1910); Phillips in Ann. S. Afr. Mus. 16: 242 (1918); Wilman, Checklist Griq. West 227 (1946); Salter in Fl. Cape Penins. 696 (1950); Jacot Guill., Fl. Lesotho 239 (1971); Ross, Fl. Natal 304 (1972); Harley in Fl. Europ. 3: 185 (1972). Type: from Europe.

M. dumetorum Schult. var. *natalensis* Briq. in Bull. Herb. Boissier 2: 702 (1894). Type: Natal, *Medly Wood* 402 (B, holo.).

Perennial rhizomatous herb; stems ascending to 0,8 m tall or trailing in water to 1,5 m long, subglabrous or sparingly to densely pubescent. *Leaves* petiolate; blade glabrous to fairly densely pubescent, freely gland-dotted on both surfaces, lanceolate to broadly ovate, 20−55 × 5−26 mm, apex acute, base cuneate to rounded, margin obscurely to distinctly toothed. *Inflorescence* terminal, of 1−3 (−4) spaced flower clusters up to 20 mm in diameter, the uppermost globose to oblong-capitate, subtended by reduced leaves (bracts), the lower clusters somewhat distant, globose, subtended by normal leaves; bracteoles linear; rhachis and pedicels subglabrous to densely pubescent. *Calyx* tubular, sparsely to densely pubescent, 3−4 mm long. *Corolla* pale to deep mauve, pinkish or purple. (Fig. 4).

Widely distributed in Europe and around the Mediterranean, extending eastwards to Siberia; found in tropical Africa from Kenya, Tanzania, Zaïre and Malawi, with a record from the swamps of northern Botswana; locally common in marshes and wet places in the higher rainfall areas of the Transvaal and adjacent parts of northern Cape and Swaziland, widespread in Natal, eastern O.F.S. and Lesotho, extending through eastern Cape, along the coast to the Peninsula and northwards along the mountains to Ceres. (Fig. 6.)

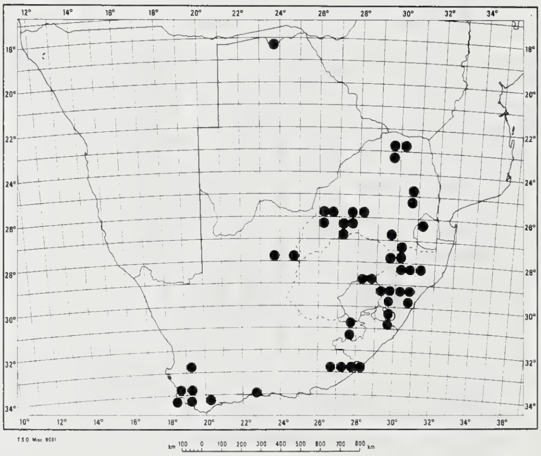


FIG. 6.— ●, *Mentha aquatica.*

There is a good deal of variation in leaf shape from lanceolate to broadly ovate, and in pubescence from glabrous (*Louw* 1391 and *Leendertz* sub TRV11519 from western Transvaal) to a densely tomentose condition (*Galpin* 14807, 14830, *Breijer* sub TRV16991 and *Mauve* 4860 from Natal). However, there is a complete range of intermediate forms and no clear geographical pattern in the variation emerges. The leaves are usually petiolate but may be subsessile in some specimens. The latter may be readily separated from *M. longifolia* and *M. spicata* by the often widely spaced, oblong to globose flower clusters with the lower clusters, when present, being subtended by normal leaves.

M. aquatica is said to have a strong minty scent and is known as Water Mint or Kruisement (Kruistement). An infusion of the leaves is taken for colds and as a tonic, being highly regarded (*Hanekom* 1379) as a treatment for promoting the flow of milk in nursing mothers.

ACKNOWLEDGEMENTS

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UITTREKSEL

Die spesies van Mentha *L. wat in suider-Afrika voorkom, is hersien en 'n sleutel vir twee inheemse en een genaturaliseerde spesies is voorsien.* M. wissii *Launert is verander na* M. longifolia *(L.) Huds. subsp.* **wissii** *(Launert) Codd.*

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The genus *Tetradenia* Benth. (Lamiaceae). I. African species

L. E. CODD*

ABSTRACT

The genus *Iboza* N. E. Br. is placed as a synonym of *Tetradenia* Benth. and the following new combinations are made: *T.* **barberae** (N.E. Br.) Codd, *T.* **brevispicata** (N.E. Br.) Codd and *T.* **riparia** (Hochst.) Codd.

INTRODUCTION

During studies in Lamiaceae for the Flora of Southern Africa it became apparent that the African genus *Iboza* N.E. Br. (1910), in which five species were originally upheld, is not generically distinct from *Tetradenia* Benth. (1830), based on a single species from the Malagasy Republic. A comparison of the two genera was facilitated by the fact that both male and female plants of a *Tetradenia* were collected by Mr D. S. Hardy and Prof. W. Rauh during their visit to the Malagasy Republic in 1969 and have flowered regularly in winter in the PRE nursery.

As well as all having a similar facies and inflorescence structure, with very small, dioecious flowers, the species now included in *Tetradenia* have a characteristic floral pattern (see Figs 2, 4 & 6):

(a) the calyx is divided nearly to the base below and consists of an upper ovate lobe and two lateral oblong lobes which are emarginate or bifid.

(b) the corolla limb is somewhat spreading and 4-lobed, with the upper lobe bifid or bilobed (sometimes giving the superficial appearance of a 5-lobed corolla), with 2 oblong lateral lobes and an oblong, slightly concave lower lobe which is slightly longer than the other three.

(c) in the male flowers there is a non-functional ovary (though *T. barberae* may be an exception in this regard) and 4 shortly exserted somewhat spreading stamens, 2 of which are ascending on each side of the upper lobe and 2 descending on each side of the lower lobe.

(d) in the female flowers there are no signs of stamens or staminodes and the style is relatively deeply bifid.

(e) the disc is produced into 1 or 2 conspicuous lobes which exceed the ovary in height (apparent also in male flowers).

(f) There are small gland-like structures at the nodes (2 below each petiole) which have not been observed in any other genus in the Lamiaceae, but which are present in all the species now included in *Tetradenia* (Fig. 1).

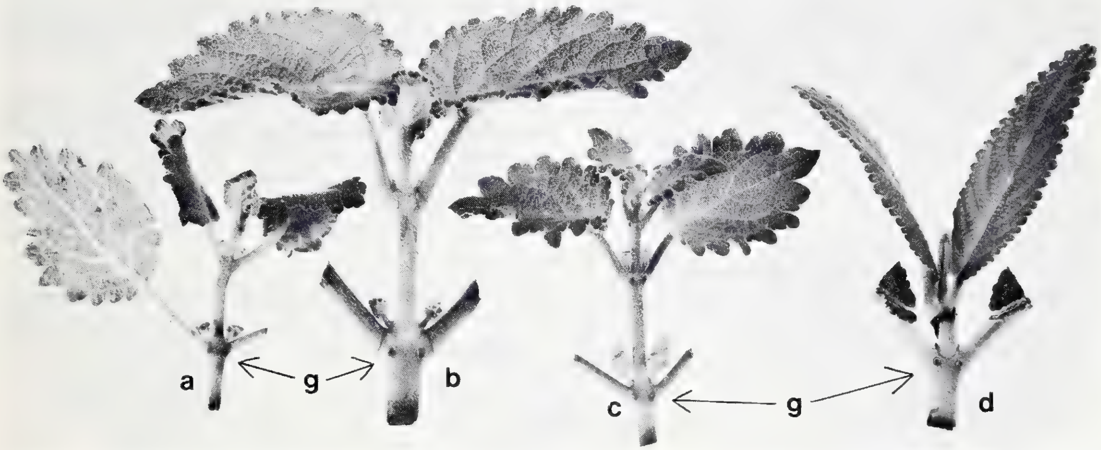

FIG. 1.—Young stems of *Tetradenia* spp. showing nodal (subpetiolar) 'glands' (g), all natural size. a, *T. brevispicata* (*Codd* 8778, from Brits); b, *T. riparia* (*Codd* 8398, from Soutpansberg); c, *T. riparia* (*De Winter* 3597, from S.W. Africa/Namibia); d, *T.* sp. (*Hardy & Rauh* 2910, from Malagasy Republic).

The nearest ally of *Tetradenia* appears to be *Mentha*, from which it differs in the more shrubby habit, dioecious flowers, and the shape of the calyx and corolla.

TETRADENIA

Tetradenia *Benth.* in Bot. Reg. sub t.1300 (1830); Lab. 164 (1833); in DC., Prodr. 12: 159 (1848); in Benth. & Hook. f., Gen. Pl. 2,2: 1180 (1876); Briq. in Natürl. Pfl.Fam. 4, 3a: 331 (1897). Type species: *T. fruticosa* Benth.

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Iboza N.E. Br. in Fl. Cap. 4,1: 298 (1910); Dyer, Gen. S. Afr. Flow. Pl. 1: 533 (1975). Lectotype (Phillips, Gen. S. Afr. Flow. Pl. 650, 1951): *I. riparia* (Hochst.) N.E. Br. (= *Moschosma riparia* Hochst.)

Moschosma Auct., non Reichb.

Perennial shrublets, soft shrubs or small trees, usually leafless or nearly so at flowering stage; stems brittle or semisucculent, at first softly glandular-pubescent and somewhat quadrangular, glabrescent and terete with age. *Leaves* small or large, those subtending inflorescence branches or secondary branches smaller towards the apex, often semisucculent, variously pubescent, crenate-dentate, aromatic. *Inflorescence* paniculate, terminal and on lateral branches, often diffusely branched, the ultimate branches spike-like (referred to as 'flower-spikes'); bracts small, ovate-deltoid to broadly ovate, imbricate in the bud stage, caducous or semipersistent. *Flowers* dioecious or occasionally bisexual *(T. barberae),* in whorls of 4–10, sessile or shortly pedicellate, dense or lax, mauve or whitish. *Calyx* minute, campanulate, 3-lobed, divided nearly to the base below, the upper lobe ovate, lateral lobes oblong, bifid or emarginate; in female flowers the calyx enlarges at maturity and the upper lobe becomes erect. *Corolla* small, tubular or funnel-shaped; limb spreading, asymmetrical, 4-lobed, lobes oblong, rounded, the upper lobe emarginate or bifid, the lowest lobe usually the longest, flat or slightly concave. *Stamens* 4, free, erect or spreading, absent in female flowers. *Disc* 1- or 2-lobed. *Ovary* present but usually infertile in male flowers (1 or 2 seeds per male flower occasionally found in *T. barberae*); style exserted, deeply bilobed in female flowers. *Nutlets* oblong-triquetrous.

Three species are recognized in Southern Africa, one of which, *T. riparia,* is very variable and extends to Angola and through east tropical Africa to Ethiopia; in addition to the type species, *T. fruticosa,* two further species from the Malagasy Republic were described by Briquet, but no material of these two species has been seen and so they are omitted from the present treatment. They will be dealt with in a subsequent article.

KEY TO SPECIES

Leaves small, ovate, 10–15 × 5–10 mm, bullate-rugose above, veins very prominent beneath; bracts ovate-deltoid, as long as broad .... 1. *T. barberae*

Leaves small or large, if less than 20 × 10 mm then not bullate-rugose above; bracts broader than long, rounded or abruptly apiculate at the apex:

  Leaves ovate-rotund, 12–30 × 10–30 mm (occasionally larger), under surface finely velvety with sessile glands and no multicellular hairs; male flower spikes 10–20 mm long .... 2. *T. brevispicata*

  Leaves variously shaped, usually longer than above, under surface sparsely to densely pubescent with stalked glands and/or multicellular hairs; male flower-spikes 10–80 mm long........ 3. *T. riparia*

These species may be fairly readily separated on vegetative characters but, in the herbarium, many flowering specimens lack leaves, or those present may be the upper leaves subtending inflorescence branches and hence smaller than usual. The male inflorescences, and especially the length and density of the 'flower-spikes' (ultimate branchlets of the inflorescence), may be of assistance in separating species, but the female 'flower-spikes' are all short and dense and seem to vary as much within a species as between species.

The floral characters are very similar in all the species and are not of much diagnostic value. In the male flowers a small infertile ovary develops (occasionally fertile in *T. barberae*), whereas in female flowers there are no signs of stamens or staminodes. Bentham, who had only a single male specimen when he described *T. fruticosa,* gave the impression that the flowers were functionally hermaphrodite.

The structure of the calyx is basically the same in all species, but shows some variation in the degree of toothing of the laterial lobes. This is best seen in the female flowers where the calyx enlarges somewhat when in fruit.

The corolla tube tends to be funnel-shaped in male flowers and smaller and more tubular in female flowers, and there is some variation between species in the length of the tube. The slightly asymmetric limb of 4 lobes (the upper lobe being emarginate or bifid may produce the effect of a 5-lobed limb) is much the same in male and female flowers of all species, with the lowest lobe longer than the others and usually shallowly concave.

Bentham drew attention to the similarity between his species and *Moschosma riparia* Hochst. but kept them in separate genera on the basis of the greater development of the disc in *T. fruticosa.* It appears that in *T. fruticosa* the disc is purple-coloured and 2-lobed whereas in the African species it is colourless and usually 1-lobed. The lobes exceed the ovary in height.

When N. E. Brown described *Iboza,* he correctly separated it from *Basilicum* Moench (= *Moschosma* Reichb.) on the dioecious flowers and the entirely different calyx and corolla, but overlooked the little-kown *Tetradenia* Benth., possibly because the description implied that the flowers were hermaphrodite.

All the indigenous species are used medicinally by native tribes in the treatment of colds and chest complaints.

1. **Tetradenia barberae** *(N.E. Br.) Codd,* comb. nov.

Iboza barberae N.E. Br. in Fl. Cap 4,1: 302 (1910). Type: 'Orange River Colony', *Mrs Barber* 7 (K, holo.!).

Twiggy shrublet 0,6–1 m tall; stems woody, terete, grey-brown, at first minutely tomentellous, lacking stipitate glands or long multicellular hairs. *Leaves* shortly petiolate; blade small, ovate, 8–15 × 5–10 mm, bullate-rugose and finely glandular-scabrous above, conspicuously veined and densely glandular-tomentellous beneath, apex obtuse, base truncate, margin crenate, thickened below; petiole 3–5 mm long. *Inflorescence* evidently coetaneous with the leaves, occasionally simple, usually with 1–3 pairs of branches near the base; terminal male flower-spikes dense, 30–95 mm long, lateral 15–55 mm long; rhachis finely and densely glandular-hispidulous; bracts ovate-deltoid, acute, 3–3,5 × 2,5–3 mm, densely tomentellous, dotted with red sessile glands; verticils usually 6-flowered; pedicels 0,5 mm long. *Calyx* 1,5 mm long, densely glandular-hispidulous, strongly ribbed; upper lobe ovate, obtuse; lateral lobes deeply toothed, giving the impression of a 5-toothed calyx, teeth 0,5 mm long. *Corolla* 3 mm long, densely pubescent without; tube narrowly funnel-shaped. *Stamens* exserted. *Disc* with 1 lobe developed beyond the infertile ovary. *Style* exserted, shortly bifid. *Female flowers* not seen, but occasional seeds are formed in the male flowers (Fig. 2).

A xerophytic shrublet of karroid Fish River scrub. The type specimen was recorded from the 'Orange River Colony', but this may be an error. The only other two gatherings seen were collected at the same time, in March 1966, as shown below.

CAPE.—3327 (Peddie): Kaffir Drift (–AC), *Tsuane A1126; Bayliss 3248.*

Evidenly a rare and distinct species, widely separated from other members of the genus. It is characterized by the uniform short dense tomentum on all parts, lacking stipitate glands and long multicellular hairs, the sparsely branched male inflorescence with relatively long, dense flower-spikes, the small ovate prominently nerved leaves which are present at flowering time, and the deeply toothed lateral calyx lobes, giving the calyx a 5-toothed appearance. The fact that 1 or 2 seeds per flower are occasionally formed in what appear to be essentially male flowers requires further study in the field. The species may be transitional between the hermaphrodite and dioecious condition. The presence of seeds can be detected by a slight increase in the size of the calyx after flowering.

2. **Tetradenia brevispicata** *(N.E. Br.) Codd*, comb. nov.

Iboza brevispicata N.E. Br. in Fl. Cap. 4,1: 302 (1910). Type: Transvaal, Wonderboom Farm near Pretoria, *Burtt Davy* 1844 (K, holo.).

Twiggy shrub or small tree 0,6–2 (–3) m tall; stems slender, woody terete, greyish-black, at first finely glandular-tomentellous, lacking stipitate glands or long multicellular hairs. *Leaves* rather small ovate-rotund to rotund, 12–30 (–55) × 10–30 (–50) mm, finely glandular-scabrous above, densely

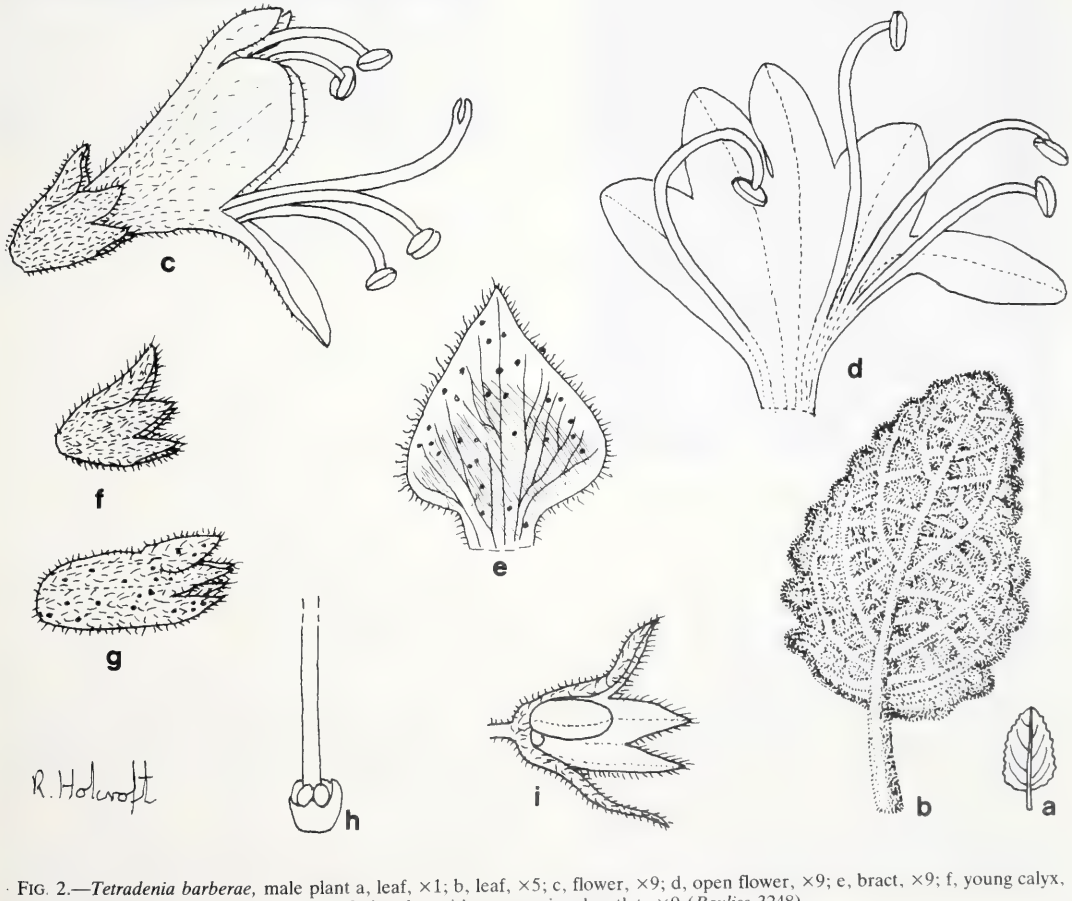

FIG. 2.—*Tetradenia barberae,* male plant a, leaf, ×1; b, leaf, ×5; c, flower, ×9; d, open flower, ×9; e, bract, ×9; f, young calyx, ×9; g, old calyx, ×9; h, ovary, ×12; i, calyx with an occasional nutlet, ×9 (*Bayliss* 3248).

glandular-tomentellous beneath, the lower surface being obscured by a short cobwebby tomentum lacking stipitate glands, the nerves often fairly prominent; apex rounded, base rounded to subcordate, margin crenate to deeply crenate-dentate; petiole 4–15 mm long. *Inflorescence* appearing after most of the leaves are shed, consisting of spikes or small panicles borne terminally and in the axils of the upper leaves, often for some distance along the stem; male and female flower-spikes dense, the male 10–20 (–25) mm long, the female shorter; rhachis densely glandular-hispidulous; bracts broadly ovate, acute, 1,5–1,75 × 1,5–2 mm, shortly tomentellous and gland-dotted, caducous; verticils usually 6-flowered; pedicels 0,5 mm long. *Calyx* densely glandular-hispidulous, 1 mm long, those of female flowers increasing in fruit to 2 mm long; upper lobe ovate, obtuse; lateral lobes shortly bifid. *Corolla* white to mauve, 2 mm long, pubescent without; tube narrowly funnel-shaped. *Stamens* slightly exserted. *Disc* 1(–)-lobed. *Style* exserted by 1 mm; style branches 0,4 mm long in female flowers, shorter in male flowers. *Nutlets* oblong, pale brown, 0,6 mm long (Figs. 3, 4).

Found in central and northern Transvaal, south-western Botswana and near Bulawayo in Zimbabwe; on dry, wooded, quartzite or granite slopes.

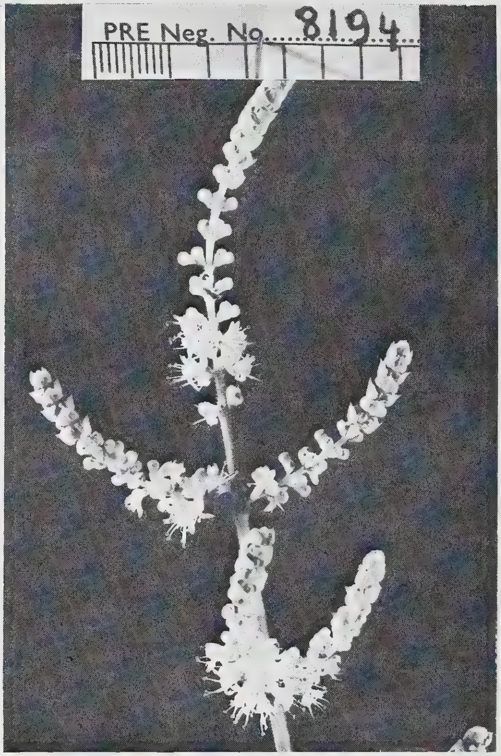

FIG. 3.—*Tetradenia brevispicata,* part of male inflorescence, slightly enlarged (*Keytel* 744).

ZIMBABWE.—2028: near Bulawayo (–AD), *Sim 19297.*

BOTSWANA.—2425 (Gaborone): 8 km S.E. of Gaborone, *Mott 396.*

TRANSVAAL.—2329 (Pietersburg): Blouberg (–AA), *Schlieben* 8616; 50 km N.E. of Pietersburg (–DA), *Fries, Norlindh & Weimarck* 2023; 29 km E. of Pietersburg (–DD), *Van Vuuren 1266.* 2429 (Zebediela): Pyramid Estate near Potgietersrus (–AA), *Galpin 8833;* Lulu Mts (–DD), *Barnard & Mogg 910; Mogg 16907; 16978;* Magnet Heights (–DD), *Barnard & Mogg 847.* 2430 (Pilgrims Rest): Schoonoord (–CA), *Barnard 223; Van Warmelo 37.* 2527 (Rustenburg): near Rustenburg (–CA), *Pegler 924; Collins sub TRV* 10522; *Story 990;*

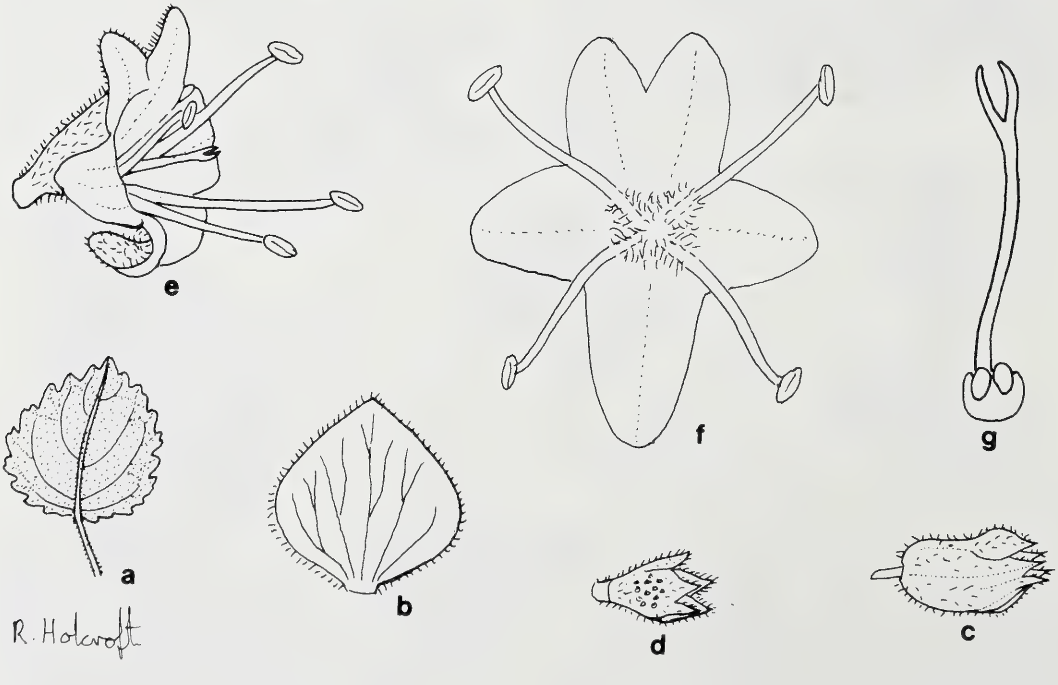

FIG. 4.—*Tetradenia brevispicata.* a, leaf, ×1; b, bract, ×8; c, mature female calyx, ×8; d, male calyx, ×8; e, male flower, ×8; f, male flower, excluding abortive ovary, ×8; g, ovary of female flower, ×20 (c and g from *Pole Evans* 3730a, remainder from *Keytel* 744).

Jacksonstuin (−DA), *Van Vuuren 312;* near Brits (−DB), *Codd 8778.* 2528 (Pretoria): Wonderboompoort (−CA), *Lanham sub TRV 37660; Louw 759; Rehmann 4508(Z).* 2529 (Witbank): 6 km N. of Lebethal Mission, Groblersdal District, *Mönnig 46.*

The species is characterized by the slender, twiggy stems with greyish-black bark, the relatively small roundish deeply crenate-dentate leaves with a fine dense tomentum on the under-surface, and the short dense male flower-spikes. The flowering period is mainly from June to September when the plants are leafless. It was first collected by Rehmann at Wonderboompoort in November−December 1879 but his specimens lacked flowers and were included in *Plectranthus grandidentatus* by Gürke (Codd in Bothalia 11: 397, 1975).

3. **Tetradenia riparia** *(Hochst.) Codd,* comb. nov.

Moschosma riparium Hochst. in Flora 28: 67 (1845); Benth. in DC., Prodr. 12: 49 (1848); Briq. in Natürl. Pfl.Fam. 4,3a: 368 (1897); Wood & Evans, Natal Pl. 1: tt.1,2 (1898); Bak. in Fl. Trop. Afr. 5: 354 (1900); Eyles in Trans. R. Soc. S. Afr. 5: 466 (1917). *Basilicum riparium* (Hochst.) Kuntze, Rev. Gen. Pl. 2: 512 (1891). *Iboza riparia* (Hochst.) N.E. Br. in Fl. Cap. 4,1: 300 (1910); Everett in Jl. N.Y. bot. Gdn 36: 12 (1935); Phillips in Flower. Pl. S. Afr. 20: t.767 (1940); Martineau, Rhod. Wild Flow. 69 (1953); Brenan in Mem. N.Y. bot Gdn 9: 39 (1954); Andrews, Flow. Pl. Sudan 3: 212 (1956); Letty, Wild Flow. Transv. 289, t.144,3 (1962); Compton, Fl. Swaz. 67,158 (1966); Launert & Schreiber in Prodr. Fl. S.W. Afr. 123: 14 (1969); Ross, Fl. Natal 306 (1972); Gibson, Wild Flow. Natal t.90,6 (1975). Type: Natal, *Krauss* 331 (MO!).

M. multiflorum Benth. in DC., Prodr. 12: 49 (1848); A. Rich., Tent. Fl. Abyss. 2: 179 (1851); Gürke in Engl., Pflanzenw. Ost-Afr. C: 349 (1895); Briq. in Natürl. Pfl.Fam. 4,39: 368 (1897); Bak. in Fl. Trop. Afr. 5: 354 (1900); Eyles in Trans. R. Soc. S. Afr. 5: 466 (1917). *Basilicum multiflorum* (Benth.) Kuntze, Rev. Gen. Pl. 2: 512 (1891). *Iboza multiflora* (Benth.) E.A. Bruce in Kew Bull. 1940: 66 (1940): Agnew, Upland Kenya Wild Flow. 642 (1974). Isotypes: Ethiopia, near Djeladjeranne, *Schimper* 766 (K!); 1688 (K!).

M. myriostachyum Benth. in Benth. & Hook. f., Gen. Pl. 2,2: 1173 (1876); Briq. in Natürl. Pfl.Fam. 4,3a: 368 (1897). *Basilicum myriostachyum* (Benth.) Kuntze, Rev. Gen. Pl. 2: 512 (1891); Hiern, Cat. Afr. Pl. Welw. 1,4: 858 (1900). Type: Zambezi region, no specimen cited.

M. urticifolium Bak. in Fl. Trop. Afr. 5: 353 (1900). *Iboza urticifolium* (Bak.) E.A. Bruce in Kew Bull. 1940: 66 (1940). Type: Tanzania, Mt Kilimanjaro, *Johnston* s.n. (K, holo.!).

Iboza galpinii N.E. Br. in Fl. Cap. 4,1: 300 (1910); Compton, Fl. Swaz. 67, 158 (1966). Type: Transvaal, near Barberton, *Galpin* 972 (K, holo.; PRE!).

I. bainesii N.E. Br. in Fl. Cap. 4,1: 301 (1910). Type: "South African Gold Fields," *Baines* s.n. (K, holo.!).

Soft shrub or small tree 1−3 (−5) m tall, freely branched; stems semisucculent, brittle, rather stout, at first 4-angled and glandular-pubescent, becoming terete and glabrous with age; bark pale brown. *Leaves* petiolate; blade ovate-oblong to rotund, 35−80 (−100) × 35−70 (−90) mm, sparsely to densely glandular-pubescent on both surfaces, on the upper-surface usually shorter and more scabrid, on the under-surface mainly restricted to the veins or stipitate-glandular to densely white tomentose over the whole surface, veins often prominent below, apex rounded, base rounded or truncate to cordate, margin coarsely crenate to crenate-dentate; petiole up to 40 mm long, densely glandular-pubescent. *Inflorescence* a terminal, usually large panicle, diffusely branched and up to 300 × 200 mm in male specimens, smaller and more compact in the female, appearing usually after the leaves are shed; inflorescence branches subtended by leaves becoming smaller towards the apex; male flower spikes dense to lax, 20−80 mm long; female flower-spikes dense, 10−25 mm long; rhachis densely glandular-pubescent; bracts broadly ovate, 1,5−2 × 2−2,5 mm, densely glandular-hispidulous, caducous; verticils 4−8 (usually 6)-flowered; pedicels 0−0,5 mm long. *Calyx* 1 mm long, densely glandular-hispidulous, expanding in female flowers to 2,5 mm. *Corolla* white to mauve, pubescent without; in the male 3−3,5 mm long, tube funnel-shaped; in the female 2−2,5 mm long, tube tubular-funnel-shaped. *Stamens* exserted. *Disc* colourless, 1-lobed. *Style* exserted by 1 mm; style branches 0,4 mm long in female flowers, shorter in male flowers. *Nutlets* oblong, pale brown, 0,6 mm long (Figs 5 & 6).

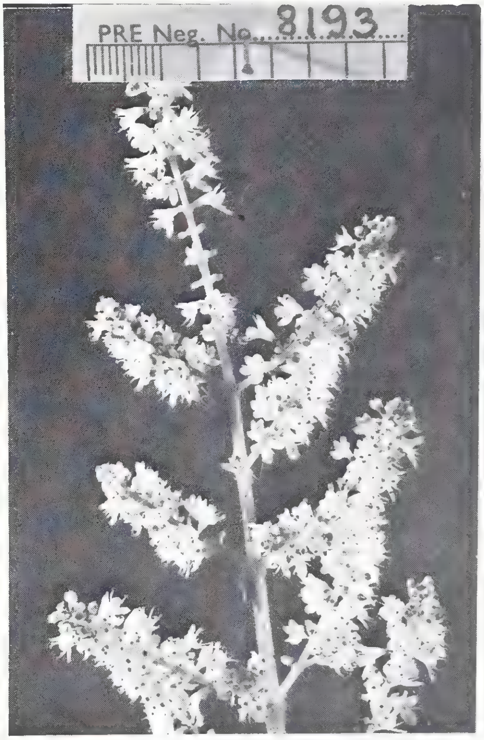

FIG. 5.—*Tetradenia riparia,* part of male inflorescence, slightly enlarged (*Codd* 8398).

Occurs in Southern Africa from coastal Natal to Swaziland, Transvaal, south-eastern Botswana and the northern half of South West Africa/Namibia, extending to Angola and through Mozambique, Zimbabwe and Zambia to Malawi, Tanzania, Kenya, Uganda, Sudan and Ethiopia. A selection of specimens from Southern Africa (usually one per degree square) is given below.

S.W.A.—1712 (Posto Velho): Otjihipa Mt (−BC), *Vahrmeijer and Du Preez 2562.* 1714 (Ruacana Falls): Ruacana Falls (−AC), *Leistner, Oliver and Vorster 322.* 1917 (Tsumeb): Farm Elandshoek (−DC), *Giess 15119.* 2114 (Uis): Brandberg (−AB), *De Winter 3597.* 2115 (Karibib): Farm Ameib. (−DC), *Giess*

15259. 2216 (Otjimbingwe): Farm Kaan Dam (−CC), *Giess 13523.* 2217 (Windhoek): Lichtenstein (−CC), *Dinter 4673.*

BOTSWANA.—2425 (Gaborone): East District (−BB), *Hansen 3435. 2525 (Mafeking): Lobatsi (−BA), Miller B1095.*

TRANSVAAL.—2229 (Waterpoort): 13 km N. of Louis Trichardt (−DD), *Van Vuuren 1230.* 2230 (Messina): Entabeni Forest Station (−CC), *Codd 8398.* 2231 (Pafuri): Punda Maria (−CA), *Van der Schijff 3151.* 2327 (Ellisras): Farm Zwarthoek 597 (−DC), *Fourie 210.* 2329 (Pietersburg): University of the North (−DC), *Bredenkamp 1087.* 2330 (Tzaneen): Duiwelskloof (−CA), *Galpin 9724.* 2428 (Nylstroom): Rietspruit, N. of Nylstroom (−CB), *Vahrmeijer 1457.* 2430 (Pilgrims Rest): Shiluvane (−AB), *Junod 538.* 2525 (Mafeking): 40 km W. of Zeerust (−BD), *Snyman 145.* 2527 (Rustenburg): Rustenburg Nature Reserve, *Jacobsen 997.* 2530 (Lydenburg): Waterval Onder (−CB), *Burtt Davy 390.* 2531 (Komatipoort): Barberton (−CC), *Galpin 972.* 2630 (Carolina): Carolina District, Arnhemburg (−AA?), *Roberts sub TRV 15852.*

SWAZILAND.—2631 (Mbabane): near Mbabane (−AC), *Compton 25131;* near Stegi (−BD), *Verdoorn 1677;* Hlatikulu (−CB), *Stewart sub TRV 9014.* 2731 (Louwsburg): Ingwavuma Poort (−BB), *Compton 30095.*

NATAL.—2732 (Ubombo): Lebombo Mts (−AC), *Ward 3449.* 2830 (Dundee): Insuzi Valley (−DB), *Acocks 12721.* 2831 (Nkandla): Eshowe District (−CD), *Venter 1675.* 2832 (Mtubatuba): Hluhluwe Game Reserve (−AA), *Ward 2625.* 2930 (Pietermaritzburg): Inanda (−BD), *Strey 8758; 8759.* 2931 (Stanger): near Durban (−CC), *Medley Wood 1001.* 3030 (Port Shepstone): Dumisa (−AD), *Rudatis 1048;* Gibraltar (−CB), *Strey 10967.*

A good deal of variation is included in the present concept of *T. riparia* but no pattern emerges and so infraspecific taxa are not upheld. In the typical form the under-surface of the leaf is thinly pubescent, with longish appressed hairs mainly on the veins. In the type of *Iboza bainesii* there is a dense white cobwebby tomentum which completely obscures the under-surface. There are, however, intermediate forms, often with numerous stipitate glands in addition to the multicellular hairs and sessile gland-dots. These are found in South West Africa/Namibia and the Transvaal, but in both

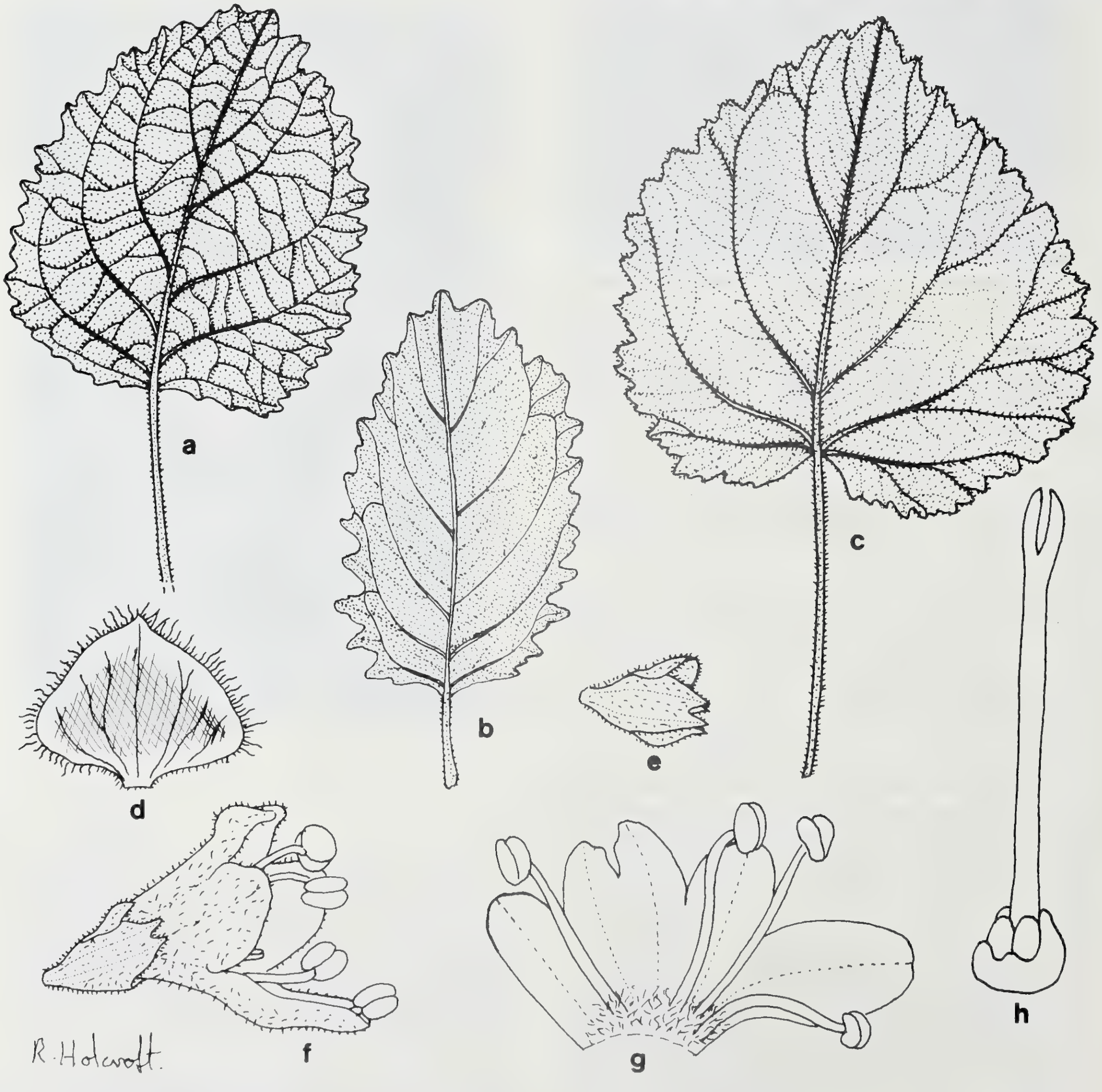

FIG. 6.—*Tetradenia riparia.* a, leaf, ×1 (*De Winter* 3597, S.W. Africa/Namibia); b, leaf, ×1 (*Junod* 538, northern Transvaal); c, leaf, ×1 (*Medley Wood* 5760, Natal); d, bract, ×9; e, calyx, ×9; f, flower, ×9; g, flower, ×9; h, abortive ovary and style, ×12 (d–h from *Codd* 8398, male plant).

territories specimens with sparse pubescence are found. The leaf-base varies from cordate to truncate or rounded independently of the degree of tomentum.

In the tropical African specimens seen there seems to be a possible link between sparse under-side leaf pubescence, lax male flower-spikes and mauve corolla on the one hand, as against densely tomentose under-side of the leaf, fairly dense male flower-spikes and whitish corolla on the other. However, most specimens either lack leaves, lack notes on corolla colour or have female flowers, and there appear to be intermediates. Also, there seems to be no association between these characters and geographic distribution. Extensive field observations are required to ascertain if the complex can be subdivided into meaningful groups.

Because of its strongly aromatic leaves, it is sometimes referred to as Ginger-bush.

UITTREKSEL

Die genus Iboza *N.E. Br. word geplaas as 'n sinoniem van* Tetradenia *Benth. en die volgende nuwe kombinasies word gemaak :* T. **barberae** *(N.E. Br.) Codd,* T. **brevispicata** *(N.E. Br.) Codd en* T. **riparia** *(Hochst.) Codd.*

Bothalia 14, 2: 185–188 (1983)

Studies in *Otiophora* Zucc. (Rubiaceae): 4. The taxonomic position of the genus

Ch. PUFF*

ABSTRACT

An evaluation of the characters of *Otiophora* provides conclusive evidence that the genus should be excluded from the Anthospermeae, the tribe in which it has traditionally been placed. Evidence from cytology, anatomy and morphology suggests a placement of the genus in the tribe Hedyotideae, in spite of some features pointing to a link with the Spermacoceae. It is, furthermore, pointed out that the tribes Spermacoceae and Hedyotideae are perhaps more closely related to each other than previously thought.

Otiophora has been placed traditionally in the tribe Anthospermeae. When Verdcourt (1950) monographed the genus, he stated (p. 35) that it 'shows affinities with *Otomeria, Pentas* (Hedyotideae) and *Pentanisia* (Knoxieae), in addition to *Anthospermum* with which it is at present classified', and thus indirectly voiced some doubt as to the true position of the genus. In his remarks on the classification of the Rubiaceae, the same author (1958) occasionally referred to *Otiophora*, but its position in the Anthospermeae was taken for granted.

There is convincing evidence, however, to show that the genus may be better placed in the Hedyotideae and so should be excluded from the Anthospermeae.

CHROMOSOME NUMBER

The chromosome number of *Otiophora* is the most convincing reason for the exclusion of the genus from the Anthospermeae. The genus has a base number of x = 17 (−18?) (Puff 1981a,b; 2n = c.36 for *O. caerulea*, Lewis, 1966). Since the most common base in the Hedyotideae is x = 9 (Lewis, 1965), that of *Otiophora* could be explained as being tetraploidic with x = 9+9−1 or 9+8. A connection to other genera or tribes with n = 17 (*Cinchona*/Cinchoneae, or *Posoqueria*, for example) is unlikely because the genus does not share any other characters. The Anthospermeae have a base number of x = 11 (Puff, 1982).

INFLORESCENCES

The inflorescences of *Otiophora* invariably consist of paired flowers arranged spirally on the inflorescence axis (Fig. 1a). This arrangement is quite different from the typical opposite arrangement of 'lateral elements' found in the vegetative region. It is a trend encountered frequently in rubiaceous inflorescences and may be explained by the unequal promotion of 'lateral elements' (lateral shoots, partial inflorescences, single flowers, etc.) originating at a node: frequently, a lateral element originates in the axil of only one of the leaves of a leaf pair at a node. If two lateral elements are produced, one is often promoted over (better developed than) the other. This is not infrequently correlated with anisophylly, whereby the promoted lateral element originates in the axil of the larger leaf (bract). The promoted lateral elements — and the larger leaves (bracts) — always seem to follow a spiral (Puff & Mantell, 1982).

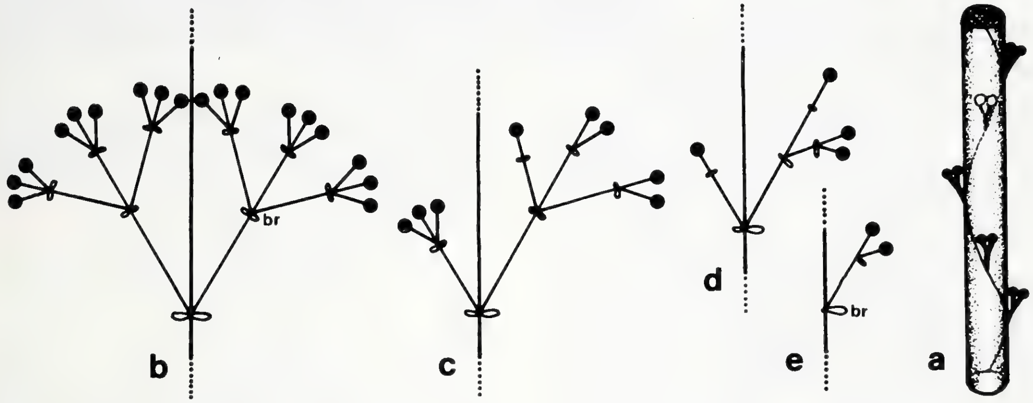

FIG. 1.— *Otiophora*, inflorescence. a, schematic representation of the paired flowers arranged spirally on the inflorescence axis; b–e, main inflorescence axis; with partial inflorescences. Theoretical derivation of two-flowered, alternately arranged partial inflorescences. e, from a typical thyrso- paniculate (see text!) inflorescence; b, (bract: br), the right partial inflorescence is gradually becoming promoted over the left one, and the axes within the partial inflorescences show unequal promotion; the promoted elements arise in the axils of larger bracts. Further explanations in the text.

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This may result in inflorescences in which (1) the partial inflorescences are monochasial [bracts-/prophylls are no longer paired at a node but solitary and arranged alternately; cincinnus and bostryx are common (Weberling, 1977)], and in which (2) the partial inflorescences themselves are alternately (spirally) arranged on the main axis of the inflorescence. Subsequently, bracts/prophylls can be suppressed altogether (as in *Otiophora*) and inflorescences become 'naked' (Troll, 1964).

The theoretical derivation of the paired flowers of *Otiophora* from a typical rubiaceous inflorescence (according to Weberling, 1977, the 'central type of rubiaceous inflorescences' is a thyrsus, but often it is a true panicle or an intermediate thyrso-paniculate inflorescence) is illustrated in Fig. 1. Although the flower pairs have ± equally long pedicels or are ± sessile, there is a strong indication that they are borne on axes (pedicels) of unequal rank: it can be observed that one flower of a pair frequently opens slightly earlier than the other.

Similar inflorescences occur in various genera of the Hedyotideae (*Pentas, Otomeria* spp., for example) and in other tribes, but are unknown in the Anthospermeae.

FLOWERS, PLACENTATION AND OVULES

The flowers of *Otiophora* are insect pollinated. Heterostyly is absent. Correlations in floral structure between *Otiophora* and the Hedyotideae are numerous: long corolla tubes with stamens inserted near the throat, long style with two filiform stigma lobes, and calyx lobes at least one of which is enlarged and foliaceous are found in genera of both tribes. There are, however, discrepancies in ovary structure and placentation.

Otiophora has only one ovule per locule, which is attached to the base of the septum. The Hedyotideae generally have many ovules per chamber that sit on an often ± spheroidal stalked placenta (Fagerlind, 1937, Fig. 19) which is inserted at the base, and sometimes to the middle of the septum. Verdcourt (1958) uses 'ovules . . . affixed to the base of the septum' as a distinguishing character of the Hedyotideae but he (1976, e.g. Figs 24 & 27) presents drawings of Hedyotideae ovaries clearly showing placentae being attached to the middle of the septum. Bremekamp (1966) states 'peltate placenta attached to the middle of the dissepiment'.

Characteristic for *Otiophora* is a stalked, shield-like placenta with a single ovule (Figs 2, 3). In literature, such shield-like structures associated with solitary ovules of various rubiaceous genera have been given different names ('strophiolum', 'obturator', 'arillus', 'extraovular growth'). It remains unknown whether they are homologous, i.e. of placental origin (Wunderlich, 1971: p. 351, for references, more detailed information and a discussion of the 'plasticity' of rubiaceous placentae and their relationship to the ovules). Such shield-like structures are absent in genera of the Anthospermeae and Paederieae (*Phyllis, Putoria*: Fagerlind 1936a, b; *Crocyllis*: Puff & Mantell, 1982; Puff, unpublished), but occur in various members of the Spermacoceae. *Diodia virginiana*, for example, (Lloyd, 1902) shows a near identical placental and ovule arrangement except that the placenta is attached to the middle of the septum. The shield-like stalked placenta of *Otiophora* may be interpreted as a reduced 'typical' (i.e. ± spheroidal, stalked) Hedyotideae placenta, in which the reduction in ovule number to one has been accompanied by a reduction in size of the originally spheroidal portion of the placenta. There, nevertheless, is still a remarkable similarity to the placentation in the Spermacoceae except for the attachment of the placenta. The latter is, by the way, much more variable in the Spermacoceae than Verdcourt (1958) and Bremekamp (1966) have led us to believe ('ovules affixed to the middle of the septum'). Placentae and ovules sometimes are also attached very near to the base of the septum (e.g. *Richardia scabra*, Verdcourt, 1976, Fig. 56). Refer, in this context, to the comments made above regarding the attachment of the ovules in the Hedyotideae.

SEEDS

As the development of the ovary of *Otiophora* continues, the ovule increases in size, while growth of placental tissue lags behind and eventually ceases. The ovule/young seed becomes much bigger than the shield- (now more rod-)like placental portion (Fig. 3) and grows around the placental tissue (Robbrecht & Puff, 1981: Fig. 4). In the mature seed, the placental tissue remains visible as a longitudinal 'ridge' on the ventral surface of the seed, although this is not always as conspicuous as shown in Fig. 4. The same phenomenon is frequently encountered in seeds of the Spermacoceae (Wunderlich, 1971, p. 352, and the literature cited there).

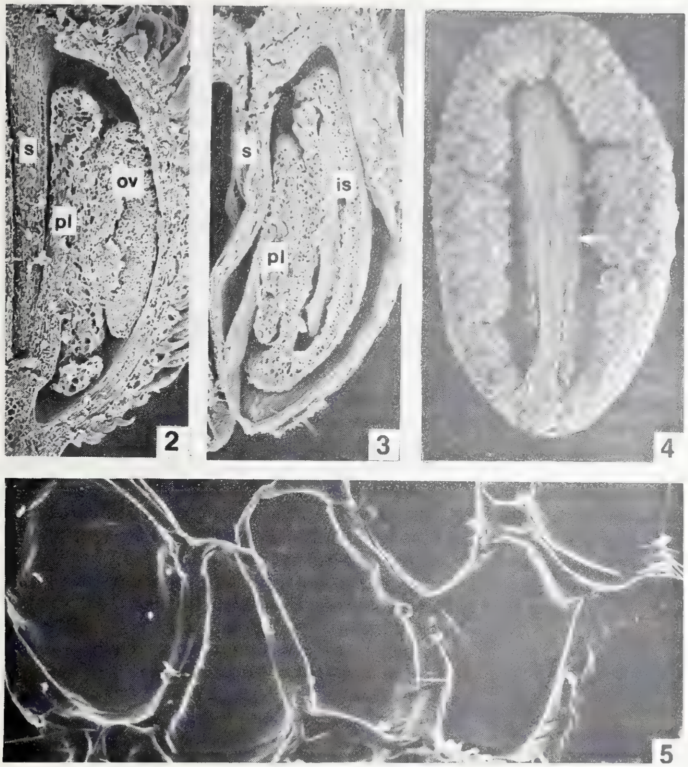
The simple testa cell structure (Fig. 5) matches that of the Hedyotideae (Bremekamp, 1952).

FRUITS

The fruit of *Otiophora* splits into two mericarps, which themselves dehisce to release the actual seeds. In contrast, the seeds of the Anthospermeae always remain enclosed in a hard endocarp, a mericarp, or the fruit as a whole (Puff, 1982). Fruits similar to those of *Otiophora* (i.e. with the same mode of dehiscence) are also found in the Hedyotidae, although capsular fruits are more common (Bremekamp, 1952). On the other hand, otiophora-like fruits are characteristic for many genera of the Spermacoceae.

POLLEN

Otiophora has subprolate to almost spheroidal, three-colporate pollen grains (Robbrecht & Puff, 1981: Figs 6, 7), the most common type found in the Rubiaceae. Such pollen grains also occur in the Hedyotideae (Lewis, 1965: subspheroidal, infrequently prolate, mostly three-aperturate; 28 African genera) and, for example, in the Anthospermeae and Paederieae (oblate, spherical to prolate, mostly three-colporate or -colpate; Robbrecht, 1982). Palynology, therefore, is of little



FIGS 2 – 5.— 2 & 3, longitudinal sections of ovary/young fruit of *Otiophora cupheoides* (South Africa, Transvaal, *Puff* 790211–1/1; SEM graphs); 2, young ovary with stalked, shield-like placenta (pl), which, at this stage of development, is larger than the ovule (ov) (s septum; c. × 55); 3, young fruit with immature seed (is; a portion of the embryo is visible); note that the placenta has remained small (c. × 35); 4, ventral view of seed of *Otiophora scabra* subsp. *scabra*; the arrow points to the remains of placental tissue (Madagascar, *Puff* 800814–3/1; SEM graph; c. × 40); 5, testa of *Otiophora angustifolia* (Zambia, *Drummond & Williamson* 10046, herb SRGH; SEM graph; c. × 535).

value to determine the taxonomic position of *Otiophora*. It should be mentioned, however, that the pollen grains of *Otiophora* differ quite clearly from those of the Spermacoceae which are mostly oblate and pluricolpate.

LEAVES AND STIPULES

Otiophora is characterized by leaves with stipules which have colleter-tipped fimbriate segments and colleters on both the inside of the stipular sheath and along its actual rim (Robbrecht & Puff, 1981: Fig. 1). According to Krause (1909), colleters are restricted to the tips of fimbriae of the much dissected stipules in the Oldenlandieae (=Hedyotideae), Knoxieae, Paederieae, Anthospermeae and Spermacoceae. This can be confirmed for the Anthospermeae and Paederieae, but it is not known whether, in addition to *Pentas lanceolata* (colleters also on the rim of the stipular sheath; Robbrecht, personal communication), there are any other species or genera in the Hedyotideae, or in any of the other tribes mentioned which, like *Otiophora*, also have colleters on the rim and on the inside of the stipular sheath. It must be kept in mind that Krause's survey was limited to relatively few genera. Judging from the wide distribution of colleters within the family it, however, remains doubtful whether this character is of any taxonomic value.

CONCLUSION

In conclusion, it can be said that (1) the genus should definitely be excluded from the Anthospermeae and that (2) it may be better placed in the Hedyotideae. It must be stressed, however, that several characters of *Otiophora* are also typical of, and point to 'cross-connections' with genera of the Spermacoceae. It appears that, without specifically considering the situation in *Otiophora*, there may be more conspicuous correlations between Spermacoceae and Hedyotideae than was originally thought. See, for example, the comments made above on the placentation in the two tribes (a discussion of other characters lies beyond the scope of this article). Perhaps the two tribes should be placed closer to each other, rather than associated with the Anthospermeae. It is suggested that the present, unsatisfactory delimitation of the two tribes be carefully reinvestigated on the basis of the many new data now available.

ACKNOWLEDGEMENTS

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UITTREKSEL

'n Evaluasie van die eienskappe van Otiophora *verskaf afdoende bewys dat die genus uitgesluit behoort te word van Anthospermeae, die tribus waarin dit tradisioneel geplaas is. Sitologiese, anatomiese en morfologiese bewyse dui op 'n plasing van die genus in die tribus Hedyotideae, ten spyte van enkele kenmerke wat dui op 'n skakel binne die Spermacoceae. Verder word dit aangedui dat die tribusse Spermacoceae en Hedyotideae moontlik nader aan mekaar verwant is as wat aanvanklik vermoed word.*

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Taxonomie numerique du genre *Eragrostis*

L. E. OHOTO-OMANA*

RÉSUMÉ

Le genre *Eragrostis,* qui a comme origine le continent africain d'après Roberty (1953), fair partie de la tribu des Eragrosteae, sous-famille des Eragrostoideae, famille des Gramineae. C'est un des genres les plus importants de la tribu, tant par le nombre de ses espèces que par les multiples usages dont on peut tirer profit.

Ce travail a pour but d'essayer de donner une classification plus naturelle des espèces du genre *Eragrostis* récoltées au Zaïre, par les méthodes statistiques actuelles. Nous avons examiné et comparé 54 espèces entre elles pour un certain nombre de caractères: 17 caractères de l'appareil végétatif, 28 de l'inflorescence, 20 caractères microscopiques de l'épiderme foliaire, et 23 caractères microscopiques de l'anatomie foliaire; les méthodes statistiques utilisées sont les méthodes dites divisives et agglomératives.

Nous n'avons pas voulu dissocier les caractères quantitatifs et qualitatifs, mais les garder ensemble dans le but d'éviter tout à priori dans le choix des caractères. Les 3 méthodes testées sont: la méthode des centres virtuels; le coefficient de similitude Sørensen; le coefficient de Gower. Seul le coefficient de Gower s'est avéré le plus adapté à nos données et a donné des résultats satisfaisants.

ABSTRACT

The genus Eragrostis *which, according to Roberty (1953), originated on the African continent, belongs to the tribe Eragrosteae, subfamily Eragrostoideae and family Gramineae. It is one of the most important genera of the Gramineae, because of the large number of species and their many uses.*

The purpose of this study is to try and provide a more natural classification of the species of Eragrostis, *collected in Zaïre, by using statistical methods. We have examined and compared 54 species with one another for a number of 'characters': 17 characters of the vegetative structure, 28 of the inflorescence, 20 microscopic characters of the leaf epidermis and 23 microscopic characters of the leaf anatomy. The methods used are divisive and agglomerative. We did not 'separate' quantitative and qualitative characters and gave the same priority rating to all characters.*

The three methods tested are: the Virtual Centres method; the similarity coefficient of Sørensen; and the coefficient of Gower. The coefficient of Gower proved to be best suited to our data and gave satisfactory results.

1. INTRODUCTION

Le genre *Eragrostis* Wolf, originaire d'Afrique (Roberty, 1953), compte 300 espèces largement réparties sur ce continent. Le genre fait partie de la sous-tribu des Eragrostineae, tribu des Eragrosteae, sous-famille des Eragrostoideae, famille des Gramineae. C'est un des genre les plus importants de la tribu, tant par le nombre de ses espèces que par multiples usages dont on peut tirer profit: *E. tef* présente une valeur céréalière surtout dans les régions arides d'Afrique; d'autres espèces telle *E. barteri* sert comme fourrage; *E. curvula* est un bon stabilisateur des sols.

Notre étude a pour but de donner une classification naturelle des espèces du genre *Eragrostis*, récoltées au Zaïre, en utilisant différentes méthodes statistiques. Nous avons examiné et comparé entre elles 54 espèces sur base de 88 caractères différents: 17 de l'appareil végétatif; 28 de l'inflorescence; 20 caractères microscopiques de l'épiderme foliaire et 23 de l'anatomie foliaire. Les 2 premiers groupes de caractères seront appelés macroscopiques et les 2 derniers, microscopiques.

La position du genre *Eragrostis* a été longtemps discutée par rapport aux tribus voisines.

Pour obtenir une classification aussi naturelle possible, on a donné la même importance à chacun des caractères retenus (cfr. listes des espèces et des caractères en Annexe, pp. 194–196).

2 LA TAXONOMIE NUMERIQUE

La taxonomie numérique est définie comme étant 'le regroupement par des méthodes numériques, d'unités taxonomiques en taxons, basé sur l'étude de leurs caractères (Sneath & Sokal, 1973).

Cette définition fait intervenir non seulement les caractères des taxons, mais également les méthodes numériques utilisées pour la répartition de ces taxons en groupes. Il faut dès le départ faire un choix des variables et des méthodes.

3 CHOIX DES CARACTERES

3.1 *Définition d'un caractère*

Le choix des caractères ou variables à prendre joue un rôle important et influence les résultats escomptés. C'est pourquoi certains auteurs conseillent de prendre le maximum de variables, tout en évitant la redondance. D'autres, en revanche, proposent un nombre plus réduit de caractères, car l'addition d'un grand nombre de variables masque souvent l'influence d'autres variables plus déterminantes.

Un caractère est le résultat d'une observation naturelle ou au moyen d'un appareil, susceptible de variation sur toute l'étendue des individus étudiés (Maréchal *et al.*, 1978).

3.2 *Qualité d'un caractère*

Un caractère se manifeste sous différents états; il peut être quantitatif, c'est-à-dire mesurable, et prendre toutes les valeurs de l'ensemble des réels.

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Il peut également être qualitatif. Dans ce cas on distingue:

- — l'ordinal: caractère qui peut être ordonné, par exemple les poils du limbe sont: abondants/ peu abondants/ pas abondants;
- — le nominal: caractère dont on ne peut mesurer les distances; par exemple: les cellules bulliformes sont du type: a/b/c/d.

Un caractère peut être alternatif: par exemple, les poils courts peuvent être présents ou absents.

4. CHOIX DES ALGORITHMES DE CLASSIFICATION

Vu le foisonnement, ces dernières années, des méthodes de classification, il a fallu faire un tri, en tenant compte de notre problème, c'est-à-dire de l'existence de variables de différents états.

Dans la classification basée sur des méthodes numériques, on distingue des méthodes dites divisives et celles dites agglomératives. Les premières (divisives) ont comme avantage le fait (qui les distingue des autres) de prendre peu de place et de temps dans la mémoire d'un programme d'ordinateur, et ensuite, certaines permettent la réallocation de l'individu déjà classé. Mais avant de procéder à l'application des trois méthodes retenues, essayons d'abord de les définir.

4.1 *'Virtual Centres' ou méthode des Centres Virtuels*

C'est une méthode divisive, itérative et polythétique permettant une réallocation des points des données et basée sur les distances euclidiennes (Berthet *et al.*, 1976). Afin de déterminer les groupes, des 'points mobiles' ou centres virtuels sont progressivement introduits dans l'espace des données; ils seront amenés à se localiser aux centres des groupes (Fig. 1).

4.2 *Le coefficient de similitude de Sørensen (par le 'nearest neighbour')*

C'est une méthode agglomérative et sert à mesurer la similitude pouvant exister entre espèces à classer (Fig. 2.).

4.3 *Le coefficient de Gower, par la méthode de 'groupement médian' (Gower, 1976a)*

C'est une méthode agglomérative, qui calcule la similitude moyenne des groupes et qui est basée sur le groupement selon l'association moyenne (Sokal & Rohlf, 1962).

4.4 *Application de ces méthodes à nos données*

Comme déjà dit, dans un souci d'objectivité, il faut essayer de rassembler le plus grand nombre de caractères possible, ce qui provoque souvent une augmentation de l'hétérogénéité des données. Pour éviter ce problème, certaines modifications ont été proposées. Soit de rendre quantitatives les variables qualitatives, soit de traiter séparément les différentes variables par des analyses successives d'abord, d'intégrer les résultats obtenus ensuite. Des trois méthodes décrites et testées, seule la dernière nous a donné des résultats satisfaisants.

- — 'Virtual Centres ou Méthode des Centres Virtuels': les résultats obtenus semblent capricieux et ininterprétables. En effet, comme le montre le graphique I, certains groupes ne contiennent qu'une seule espèce: tels les groupes n° 3, 4, 5 et 6; alors que d'autres accumulent plus de la moitié des espèces: tel par exemple le groupe n° 1.
- — Le coefficient de similitude de Sørensen: le dendrogramme. Il est obtenu à l'allure d'escalier. Les espèces se regroupent par enchaînement, alors que nous nous attendions à la formation des groupes plus ou moins distincts.
- — Le coefficient de Gower (dendrogrammes: Figs 3, 4 et 5): s'est avéré le plus efficace et adapté à

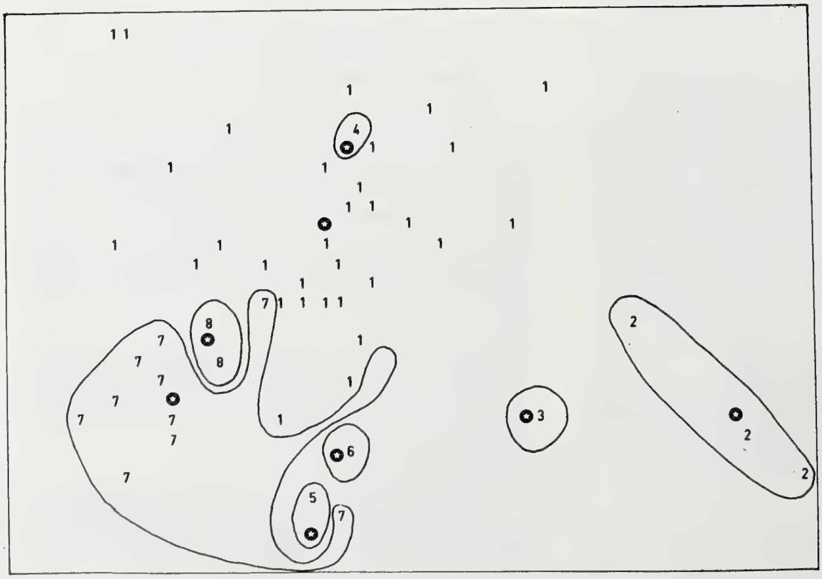

FIG. 1.—Groupes obtenus par la methode des centres virtuels.

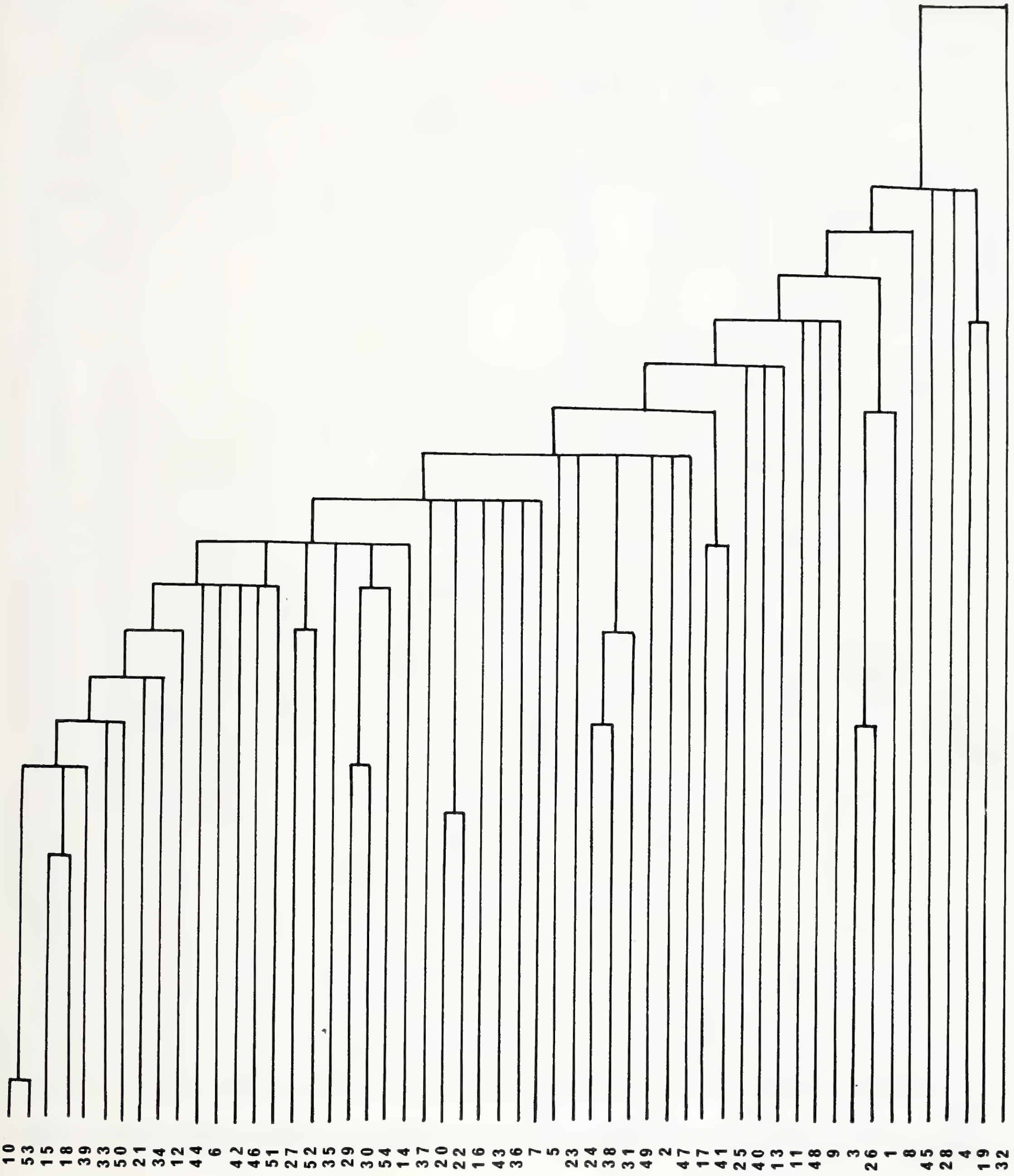

FIG. 2.—Dendrogramme relatif a la methode de Sørensen: l'ensemble des caractères.

nos données. En effet, il est applicable à tous les types de caractères, quel que soit leur état et surtout il fait ressortir les contrastes entre les groupes principaux.

5. CONCLUSION

Des trois méthodes testées, seul le coefficient de Gower a donné des résultats satisfaisants. Les espèces ont été réparties en 8 groupes principaux naturels. Cependant, les groupes ainsi obtenus présentaient quelque hétérogéinéité. Une analyse assez approfondie, ainsi qu'une certaine hiérarchisation des caractères, ont été jugées nécessaires. De même, un certain nombre de caractères ont été éliminés, du fait qu'ils présentaient, soit une grande variation individuelle ou spécifique (en ce qui concerne les variables quantitatives), soit une trop grande discrimination au niveau des groupes (pour les variables qualitatives). Finalement, c'est sur base de 66 caractères que les groupes ont été obtenus.

(Voir liste des groupes en annexe).

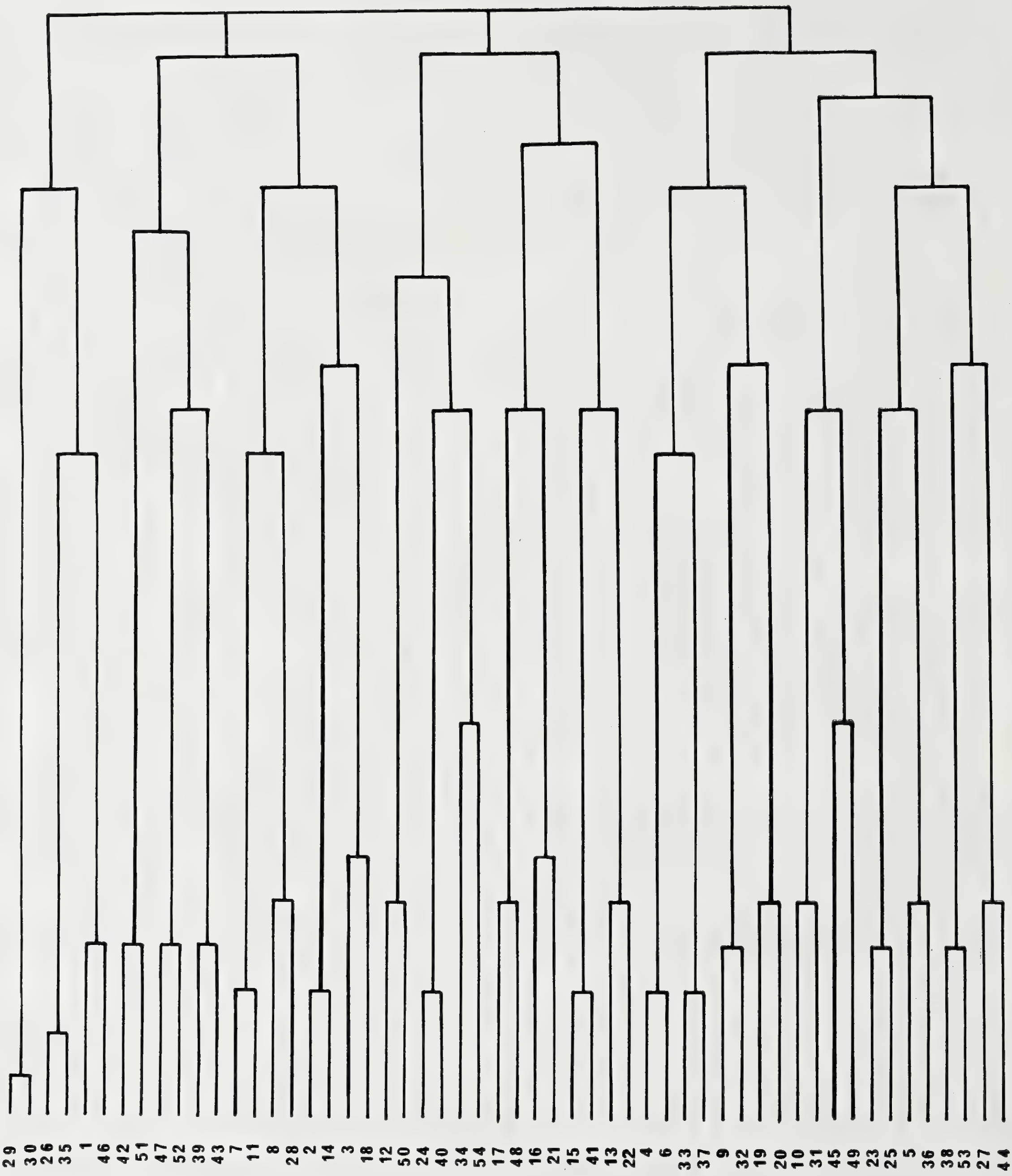

FIG. 3.—Dendogramme relatif a la methode de Gower: caracteres macroscopiques.

UITTREKSEL

Die genus Eragrostis, *wat volgens Roberty (1953) sy oorsprong in Afrika gehad het, behoort aan die tribus Eragrosteae, sub-familie Eragrostideae en familie Gramineae. Dit is een van die belangrikste genera van die Gramineae vanweë die groot aantal spesies en hul baie gebruike.*

Die doel van hierdie studie is om 'n meer natuurlike klassifikasie van die Eragrostis-*spesies wat in Zaïre versamel is te probeer voorsien deur die gebruik van statistiese metodes. Ons het 54 spesies ondersoek en met mekaar vergelyk vir 'n aantal 'kenmerke': 17 kenmerke van die vegetatiewe struktuur, 28 van die bloeiwyse, 20 mikroskopiese kenmerke van die blaarepidermis en 23 mikroskopiese kenmerke van die blaaranatomie. Die metodes wat gebruik is, is verdelend en groepvormend. Ons het nie kwantitatiewe en kwalitatiewe kenmerke 'geskei' nie en het aan alle stappe dieselfde rangorde gegee.*

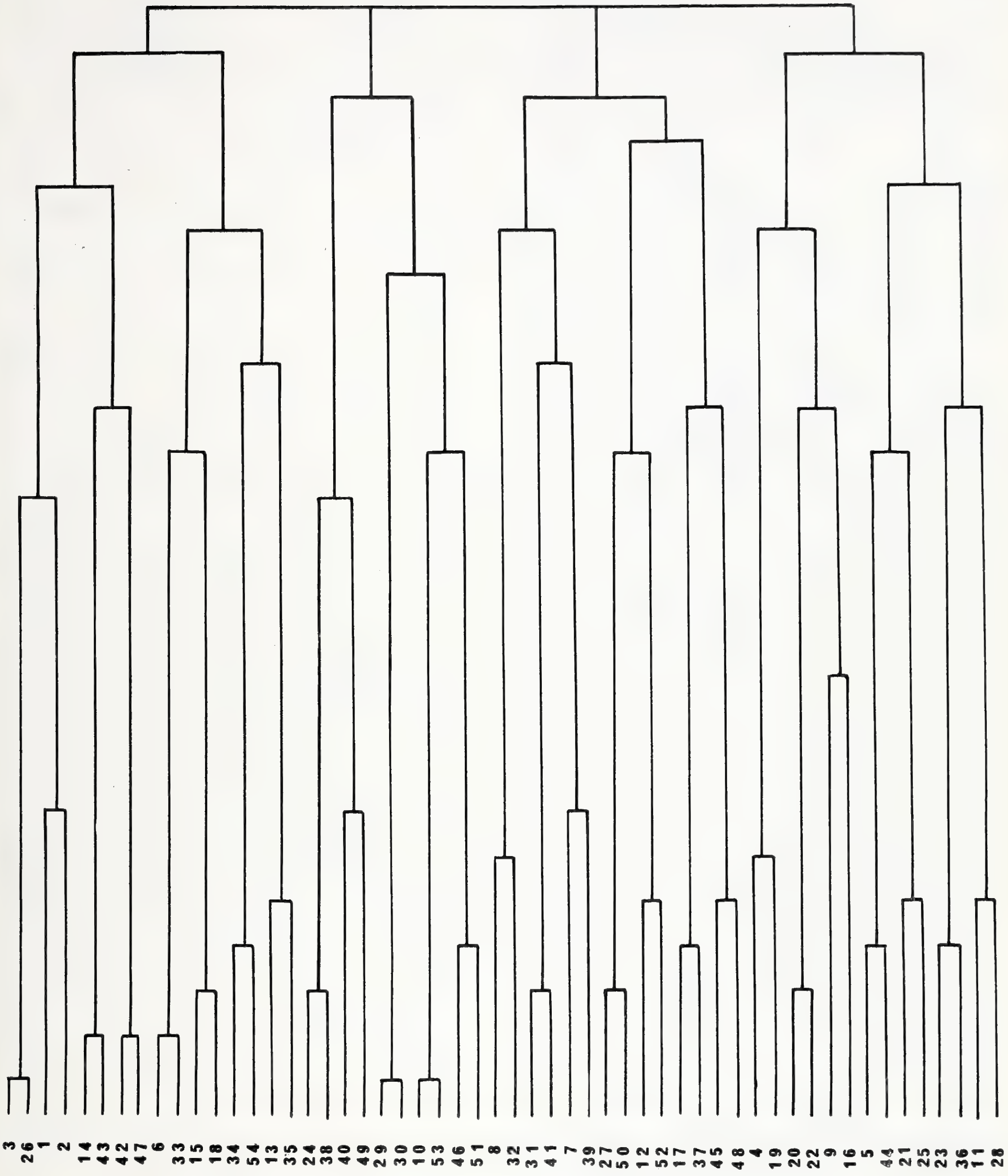

FIG. 4.—Dendogramme relatif a la methode de Gower: caracteres microscopiques.

Die drie getoetste metodes is: die 'Virtual Centres'-metode; die gelyksoortige koëffisiënt van Sørensen; en die koëffisiënt van Gower. Die koëffisiënt van Gower was die geskikste vir ons data en het bevredigende resultate gelewer.

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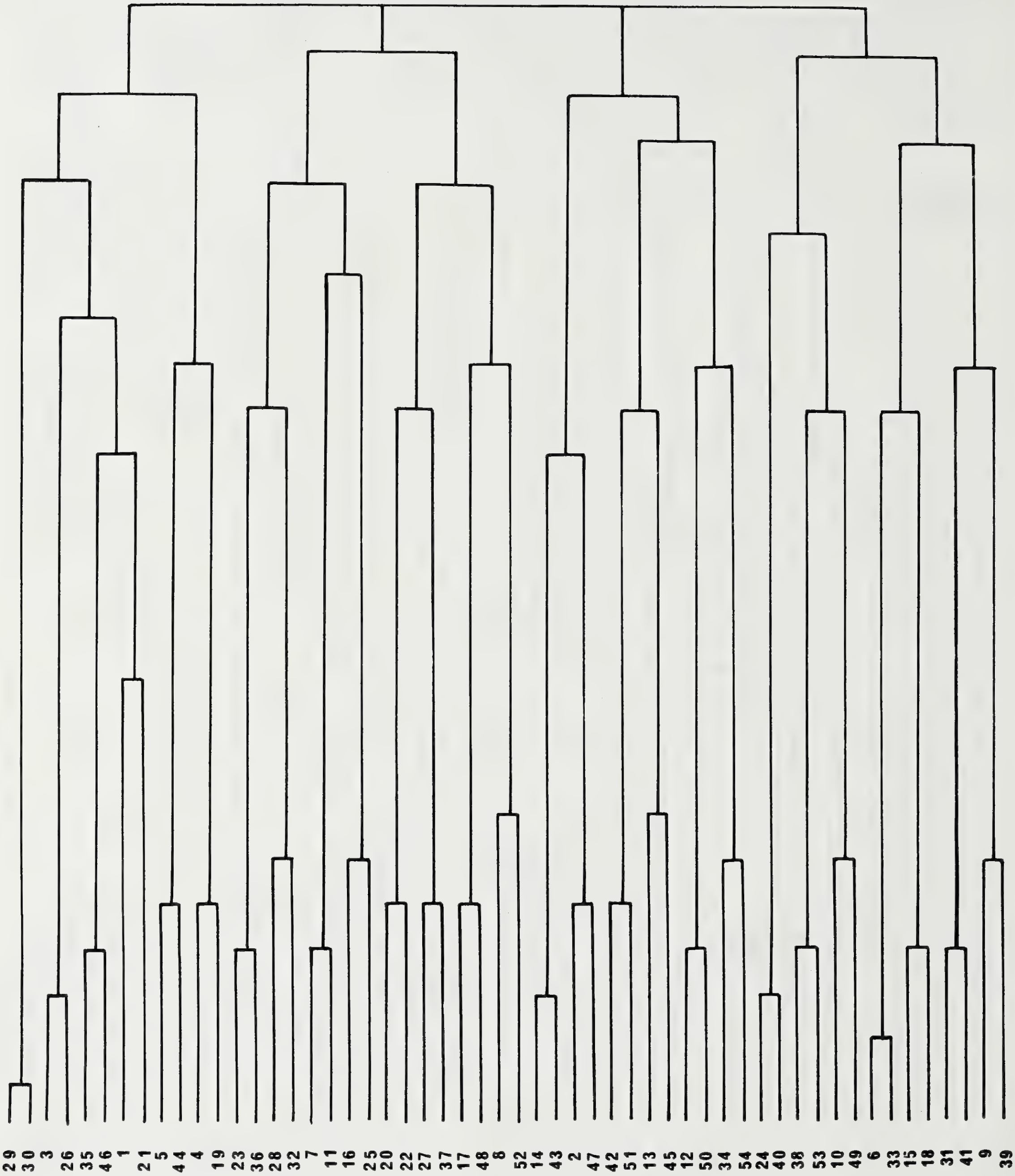

FIG. 5.—Dendogramme relatif a la methode de Gower: l'ensemble des caractères.

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ANNEXE

LISTES DES ESPÈCES DU GENRE *ERAGROSTIS*

1. *E. aethiopica* Chiov.
2. *E. arenicola* C. E. Hubbard
3. *E. aspera* Nees
4. *E. atrovirens* (Desf.) Trin. ex Steud.
5. *E. barteri* C. E. Hubbard
6. *E. botryodes* W. D. Clayton
7. *E. caespitosa* Chiov.
8. *E. canescens* C. E. Hubbard
9. *E. caniflora* Rendle
10. *E. capensis* (Thund.) Trin.
11. *E. castellaneana* Buscal. & Muschl.
12. *E. chapelieri* (Kunth) Nees
13. *E. cilianensis* (All.) Lutati
14. *E. ciliaris* (L.) R. Br.
15. *E. congesta* Oliv.

16. *E. curvula* (Schrad.) Nees
17. *E. cylindriflora* Hochst.
18. *E. exasperata* Peter
19. *E. gangetica* (Roxb.) Steud.
20. *E. heteromera* Stapf
21. *E. homblei* De Wild.
22. *E. humidicola* Napper
23. *E. inamoena* K. Schum.
24. *E. kiwuensis* Jedw.
25. *E. lappula* Nees
26. *E. macilenta* (A. Rich.) Steud.
27. *E. mildbraedii* Pilg.
28. *E. mollior* Pilg.
29. *E. namaquensis* Schrad.
30. *E. namaquensis* Schrad. var. *diplachnoides* (Steud.) W. D. Clayton
31. *E. nindensis* Ficalho & Hiern
32. *E. olivacea* K. Schum.
33. *E. paniciformis* (A. Br.) Steud.
34. *E. patens* Oliv.
35. *E. pilosa* (L.) P. Beauv.
36. *E. plurigluma* C. E. Hubbard
37. *E. prolifera* (Sw.) Steud.
38. *E. racemosa* (Thunb.) Steud.
39. *E. rejuvenescens* Rendle
40. *E. schweinfurthii* Chiov.
41. *E. sclerantha* Nees subsp. *villosipes* (Jedw.) Launert
42. *E. scotelliana* Rendle
43. *E. setulifera* Pilg.
44. *E. squamata* (Lam.) Steud.
45. *E. tef* (Zucc.) Trotter
46. *E. tenella* (L.) Roem. & Schult.
47. *E. tenuifolia* (A. Rich.) Hochst. ex Steud.
48. *E. thollonii* Franch.
49. *E. tremula* Steud.
50. *E. turgida* (Schumach.) de Wild.
51. *E. viscosa* (Retz.) Trin.
52. *E. volkensii* Pilg.
53. *E. welwitschii* Rendle

LISTE DES CARACTERES

1. Plante vivace / annuelle
2. Plante stolonifère / cespiteuse
3. Port dressé / génïculé
4. Habitat sec / humide
5. Nombre de noeuds:
6. Taille moyenne de la plante:
7. Noeuds engainés / pas
8. Limbe: longuer:
9. Limbe: largeur:
10. Limbe: rubané/ lancéolé
11. Limbe: base: largeur <ou> que la gaine
12. Limbe: poile grands/ petits/ pas
13. Limbe: marge: lisse/ scabre
14. Limbe: marge: avec glandes/ sans glandes
15. Epiderme supérieur: lisse/ scabre
16. Ligule: poils: abondants/ peu/ pas
17. Nervure principale: proéminente/ peu/ pas
18. Epillet sessile ou a` pédicelles 5 mm/ pédicelles> 5 mm
19. Panicule: lâche/ contractée/ spiciforme
20. Panicule: longueur:
21. Rachis: droit/ en zigzag
22. Rachis: glabre/ pubescent
23. Rachis: persistant/ caduc
24. Rachis avec glandes/ sans glandes
25. Rachis et rachéoles: scabres/ lisses
26. Désarticulation de bas vers le haut/ inverse
27. Epillet: longueur:
28. Epillet: largeur:
29. Epilett: nombre de fleurs:
30. Epillet: couleur: pâle/ vert foncé/ violette
31. Epillet: forme: lancéolé-linéaire/ ovale-arrondie
32. Rachéole dans épillet; visible/ pas
33. Glume inférieure: longueur:
34. Glume supérieure: longueur:
35. Lema: longueur:
36. Palé: longueur:
37. Glumelles: ciliées/ pas
38. Paléa: persistante/ caduque
39. Lemma: nervure médiane scabre/ lisse
40. Nombre d'étamines: 2/”^{3}
41. Anthères: longueur:
42. Caryopse: longueur:
43. Caryopse: L/l (Rapport Longueur sur largeur)
44. Caryopse: couleur: brune/ pâle/ blanche
45. Caryopse: forme: aplatie/ pas
46. Cryptes dans l'épiderme abaxial: présentes/ absentes
47. Nervure principale: différente des autres/ pas
48. Nervure principale: avec parenchyme incolore/ pas
49. Nervure principale: avec bande fibreuse continue sous la face adaxiale/ pas
50. Aiguillons sur épiderme adaxial: beaucoup/ peu/ pas
51. Aiguillons sur épiderme abaxial: présents/ absents
52. Fibres extrafasciculaires sur les bords: beaucoup/ peu/ pas
53. Fibres extrafasciculaires sous l'épiderme adaxial: beaucoup/ peu/ pas
54. Epaisseur du limbe au niveau d'un faisceau de premier ordre:
55. Gaine parenchymateuse I: développement:
56. Gaine parenchymateuse II: forme: a/b/c/d
57. Gaine fibreuse/ complète/ pas
58. Cellules bulliformes: développement:
59. Cellules bulliformes: forme: a/b/c/d
60. Faisceau: nombre total
61. Faisceau de 1er ordre: nombre
62. Faisceau de 2ème ordre: nombre
63. Faisceau de 3ème ordre: nombre
64. Rapport entre le nombre total des faisceaux et le nombre de faisceau de 1er ordre:
65. Rapport entre l'épaisseur du limbe au niveau d'un faisceau de 1er ordre et l'épaisseur du limbe au niveau du mésophylle adjacent:
66. Faisceaux de 1er ordre: forme: circulaire/ elliptique/ angulaire
67. Epiderme abaxial: ondulé: fortement/ peu/ pas

68. Epiderme adaxial à côtes: proéminents: très/ peu/ pas
69. Nombre de files stomatiques: une/ plusieurs
70. Files stomatiques: juxtaposées/ pas
71. Cellules subsidiaires: forme: triangulaire/ en dôme
72. Stomates: dimensions:
73. Aiguillons: abondants peu/ pas
74. Aiguillons: pointe: arrondie/ pas
75. Aiguillons: position: allongée/ pas
76. Aiguillons: base: arrondie/ pas
77. Poils courts: abondants/ peu/ pas
78. Poils courts: longueur:
79. Poils courts: cellule distale = ou cellule basale
80. Poils courts: base: effilée/ pas
81. Poils courts: bicellulaires/ unicellulaires
82. Poils longs: présents/ absents
83. Cellules courtes sur zone intercostale: abondantes/ peu/ pas
84. Cellules courtes: grand axe: vertical/ horizontal
85. Cellules courtes: isolées/ groupées
86. Cellules siliceuses: forme a/b/c/d
87. Cellules épidermiques: parois: très sinueuse/ peu sinueuse
88. Densité stomatique

LISTE DES GROUPES

Groupe I: composé de:
E. aethiopica
E. aspera
E. macilenta
E. namaquensis
E. namaquensis var. *diplachnoides*
E. pilosa
E. tef

Groupe II: composé de:
E. atrovirens
E. barteri
E. curvula
E. gangetica
E. heteromera
E. caniflora
E. homblei
E. humidicola
E. lappula
E. squamata

Groupe III: composé de:
E. caespitosa
E. castellaneana
E. inamoena
E. mollior
E. nindensis
E. olivacea
E. plurigluma
E. rejuvenescens
E. sclerantha subsp. *villosipes*

Groupe IV: composé de:
E. canescens
E. cylindriflora
E. mildbraedii
E. prolifera
E. tenuifolia
E. viscosa

Groupe V: composé de:
E. arenicola
E. ciliaris
E. setulifera
E. tenella

Groupe VI: composé de:
E. chapelieri
E. cilianensis
E. patens
E. scotelliana
E. superba
E. tremula
E. turgida
E. welwitschii

Group VII: composé de:
E. capensis
E. kiwuensis
E. racemosa
E. schweinfurthii
E. thollonii
E. volkensii

Groupe VIII: composé de:
E. botryodes
E. congesta
E. exasperata
E. paniciformis

Bothalia 14, 2: 197–203 (1983)

Leaf anatomy of the South African Danthonieae (Poaceae). VII. *Merxmuellera decora, M. lupulina* and *M. rufa*

R. P. ELLIS*

ABSTRACT

The leaf anatomy of *Merxmuellera decora* (Nees) Conert, *M. lupulina* (Thunb.) Conert and *M. rufa* (Nees) Conert is described and illustrated. The epidermal structure is shown to be uniform in all three taxa and to be unique in the genus. The leaf anatomy is very variable and three distinct types are evident. *M. lupulina* is consistent, but all three anatomical types are represented in the samples examined of both *M. decora* and *M. rufa*. The anatomical types show similarities with *Pentaschistis involuta (*Steud.) Adamson, *M. dura* (Stapf) Conert, *M. stricta* (Schrad.) Conert and *M. disticha* (Nees) Conert. *M. decora, M. lupulina* and *M. rufa,* together with *P. involuta,* therefore, appear to form a recognizable group intermediate between *Pentaschistis* and *Merxmuellera.*

INTRODUCTION

These three danthonoid grass species were not included in the genus *Merxmuellera* in the original description (Conert, 1970). Later, however, they were referred to *Merxmuellera* as *M. decora* (Nees) Conert (= *Danthonia zeyheriana* Steud.), *M. lupulina* (Thunb.) Conert [= *D. lupulina* (Thunb.) Beauv. ex Roem. & Schult.] and *M. rufa* (Nees) Conert [= *D. lanata* (Schrad.) Schrad. and *D. macrocephala* Stapf] (Conert, 1971).

Morphologically these species comprise a distinct group within *Merxmuellera* and can easily be distinguished from the 14 other species of this genus. They are all strong perennials with distinctly bulbous bases consisting of the old woolly leaf sheaths which are deeply sunken into the ground. In addition, the lower, and, sometimes, even the upper leaf sheaths, are covered with woolly hairs on the outer surface. This wooliness is not found in any other *Merxmuellera* species (Chippindall, 1955). All these species are obviously fire-adapted and commonly occur in firebreaks and are particularly conspicuous after burns. They occur on mountain slopes from the Cape Peninsula as far east as Knysna — being restricted to the extreme south of the African continent.

Although these species form a homogeneous morphological entity they are difficult to separate from one another satisfactorily. *M. rufa,* in particular, is a variable taxon where all specimens intermediate between *M. lupulina* and *M. decora* are accommodated. Size of spikelets and degree of branching of the inflorescence is particularly variable and a hybrid origin appears to be indicated.

Anatomy, to some extent, confirms these morphological indications and confirms the morphological relationships of *M. rufa* with either *M. decora* or *M. lupulina.* In addition, the leaf anatomy reveals that at least three separate taxa are referred to *M. decora* and that *M. lupulina* shows very close similarities with some *Pentaschistis* species, in particular *P. involuta* (Steud.) Adamson. Anatomically these species are, therefore, very variable with virtually every population differing in leaf anatomy, especially of the leaf as seen in transverse section. This makes specific descriptions of the leaf anatomy largely meaningless and, consequently, only abbreviated anatomical descriptions are given. The terminology adopted by Ellis (1976, 1979) will be used for the descriptions together with the following abbreviations:

vb/s—vascular bundle/s
1'vb/s—first order vascular bundle/s
3'vb/s—third order vascular bundle/s
ibs—inner bundle sheath; mestome sheath
obs—outer bundle sheath; parenchyma sheath

ANATOMICAL DESCRIPTION OF *MERXMUELLERA DECORA*

In the sample studied three distinct anatomical types can be distinguished.

Type 1 (Figs 1 & 2)

Leaf outline: permanently infolded with elliptical outline (Figs 1 & 2); channel width somewhat variable; leaf width markedly greater in centre of lamina (Fig. 1). *Ribs and furrows:* adaxial furrows deep and cleft like; present between all vbs; ribs rounded with vertical sides. Abaxial ribs and furrows well developed on either side of the median vb and adjacent one (Fig. 2) or two (Fig. 1) vbs. This character is diagnostic for this type of *M. decora. Median vascular bundle:* similar to lateral 1'vbs. *Vascular bundle arrangement and structure:* 9 or 11 vbs in section; 1 3'vb between successive 1'vbs; all bundles circular and without sclerified tissue in the phloem. *Vascular bundle sheaths:* obs cells round and without chloroplasts; sheath circular and entire except for abaxial interruption in 1'vbs; adaxial extensions consist of parenchyma cells intergrading into the sclerenchyma girder (Fig. 1). Ibs complete in 1'vbs but reduced in 3'vbs. *Sclerenchyma:* adaxial girders inversely anchor-shaped; abaxial girders trapezoidal. *Mesophyll:* small, tightly packed, isodiametric cells in X-shaped groups; no colourless cells. *Adaxial epidermis:* small bulliform cells at bases of all furrows. *Abaxial epidermis:* small bulliform cells at bases of furrows; costal epidermis cells large, regular; no macro-hairs, prickles or papillae.

Type 2 (Fig.3)

Leaf outline: permanently infolded with elongated elliptical outline (Fig. 3); adaxial channel a

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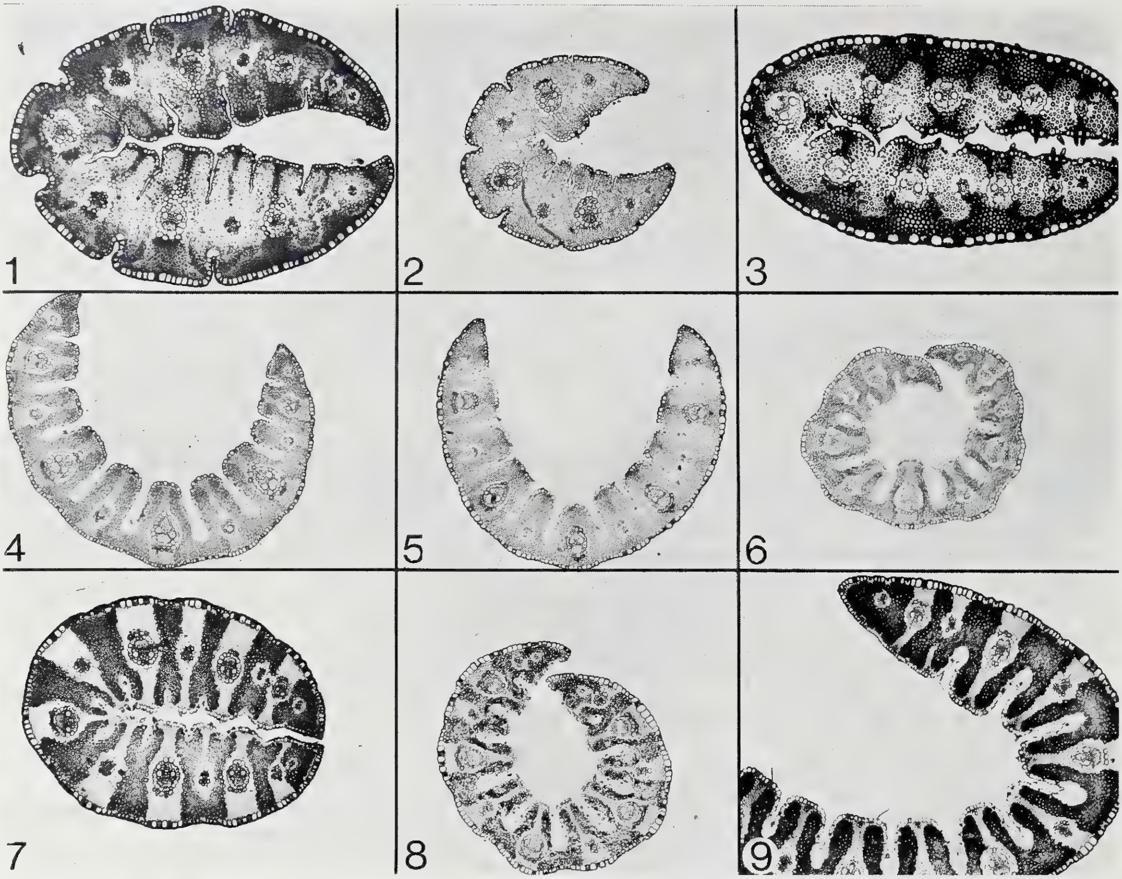


FIGS 1–9.—Leaf blade outline in transverse section. 1–3, *Merxmuellera decora.* All setaceous, permanently infolded leaves: 1, *Ellis* 2543, × 100; 2, *Ellis* 657, × 100; 3, *Ellis* 2553, × 160. 4–6, *Merxmuellera lupulina.* Inrolled leaves that can expand. All × 100: 4, *Ellis* 2254; 5, *Ellis* 2256; 6, *Taylor* 4513. 7–9, *Merxmuellera rufa.* Variable leaf outline. All × 100: 7, *Ellis* 2517; 8, *Kruger* 491; 9, *Ellis* 2483.

narrow cleft; leaf width not markedly thicker in centre of lamina as in Type 1. *Ribs and furrows:* adaxial furrows shallow, cleft-like becoming reduced towards the margin; present between all vbs. Abaxial ribs and furrows absent in contrast to Type 1. *Median vascular bundle:* similar in size and shape to lateral 1'vbs. *Vascular bundle arrangement:* 9–11 vbs in section. Lateral 1'vbs not interspaced by 3'vbs as in Type 1. *Vascular bundle structure:* similar to Type 1. *Vascular bundle sheaths:* broad adaxial and abaxial interruptions present; no bundle sheath extensions present. *Sclerenchyma:* adaxial girders inversely anchor-shaped with short thick stems; abaxial sclerenchyma continuous sub-epidermal band of varying thickness, with large trapezoidal girders extending to, and interrupting the obs. *Mesophyll:* small, tightly packed, isodiametric cells in Y-shaped groups (not X-shaped as in Type 1); no colourless cells. *Adaxial epidermis:* very small bulliform cells at bases of all furrows. *Abaxial epidermis:* no bulliform cells; epidermal cells of regular size and shape with outer periclinal wall thickened and covered by continuous, thickened cuticle; no macrohairs, prickles or papillae.

Type 3

Virtually identical to *M. lupulina* and the relevant description will suffice.

ANATOMICAL DESCRIPTION OF *MERXMUELLERA LUPULINA*

The anatomy of the leaf as seen in transverse section is remarkably consistent in the sample studied. This is Type 3 of Table 1.

Leaf outline: not permanently infolded; loosely involutely inrolled (Figs 4–6); 11 vbs in section in all specimens except van Rensburg *199* which has 19. *Ribs and furrows:* medium, narrow to cleft-like adaxial furrows present between all vbs; ribs rounded but with vertical sides; all ribs similar in shape. No abaxial ribs or furrows developed. *Median vascular bundle:* indistinguishable structurally from the lateral 1'vbs. *Vascular bundle arrangement:* 1'vbs and 3'vbs alternate; 1'vbs centrally positioned but 3'vbs located slightly towards the abaxial side (Figs 4 & 5). *Vascular bundle structure:* 1'vbs and 3'vbs circular in outline;

narrow xylem vessels; no sclerosed phloem. *Vascular bundle sheaths:* obs round; adaxial and abaxial interruptions; no extensions. Obs cells colourless, thinwalled and rather small; not conspicuous. Ibs entire; walls heavily but uniformly thickened. *Sclerenchyma:* adaxial girders inversely anchor-shaped; stem long and thin; trapezoidal abaxial girders (Figs 4 & 5). All fibres of girders of cellulose as they only stain green with fast green and safranin. This is exceptional in the genus *Merxmuellera* where sclerenchyma is always lignified. *Mesophyll:* not radiate; homogeneous, regular, small cells tightly packed, no colourless cells. *Adaxial epidermis:* bulliform cells well developed; fan-shaped; situated at bases of furrows. Few hooks present. *Abaxial epidermis:* epidermal cells of regular size and shape with outer periclinal wall somewhat thickened and covered by a continuous cuticle; no epidermal appendages or bulliform cells.

ANATOMICAL DESCRIPTION OF *MERXMUELLERA RUFA*

Anatomy extremely variable and intergrades with both Types 1 and 2 of *M. decora* as well as *M. lupulina*. For convenience, these three types will be briefly described separately.

Type 1

Resembles Type 1 of *M. decora* closely in that abaxial grooves are developed. These grooves are cleft-like and tend to fade toward the margin. The only appreciable difference is that these specimens do not seem to have permanently infolded leaves but show a tendency to be able to open to a certain degree. In addition, the adaxial ribs are not as regular as in *M. decora* but ribs associated with 1'vbs tend to be massive and those overlying 3'vbs triangular.

Type 2 (Fig. 7)

Permanently infolded type without abaxial ribs and furrows. In all specimens 1'vbs alternate with 3'vbs (Fig. 7), whereas in the *M. decora* type which this resembles (Fig. 3), there are successive 1'vbs situated laterally. Obviously this type intergrades with the next type which has a more open leaf (Fig. 9).

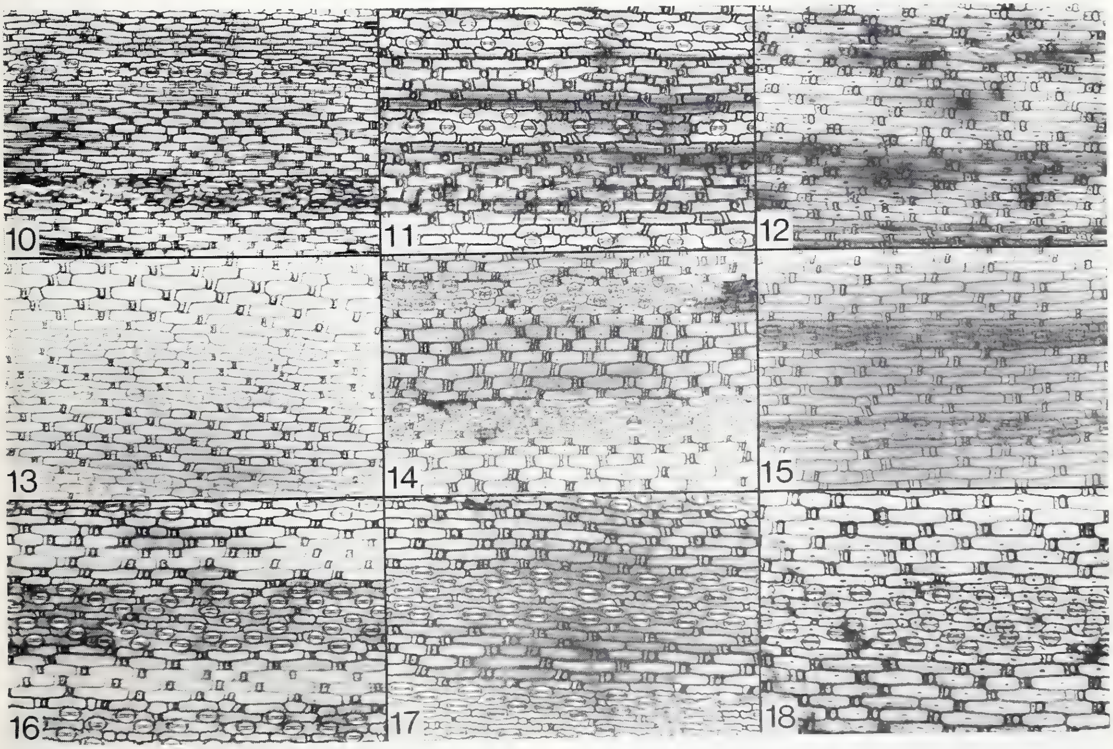
Type 3 (Figs 8 & 9)

All specimens conform to the description of *M. lupulina* very closely. The only deviation observed is in one specimen where the sclerenchyma is lignified (Fig. 9) and not of cellulose (Fig. 8). Due to staining, this difference is enhanced but structurally there is actually very little difference.

COMBINED DESCRIPTION OF EPIDERMAL HISTOLOGY OF *MERXMUELLERA DECORA*, *M. LUPULINA* AND *M. RUFA*

Abaxial epidermis

Intercostal zone: present in all specimens except Type 2 of *M. decora* (Fig. 12) where it is absent due



FIGS 10–18.—Abaxial epidermis as seen in surface view. 10–12, *Merxmuellera decora:* 10, *Ellis* 2543, × 160; 11, *Ellis* 2553, × 250; 12, *Ellis* 657, × 250. 13–15, *Merxmuellera lupulina.* All × 250: 13, *Ellis* 2254; 14, *Ellis* 2256; 15, *Taylor* 5477. 16–18, *Merxmuellera rufa.* All × 250: 16, *Ellis* 2483; 17, *Ellis* 2517; 18, *Ellis* 1190.

to development of hypodermal sclerenchyma (Fig. 3); in Type 2 of *M. rufa* girders do not fuse (Fig. 7) and intercostal zones are present (Fig. 17); present in abaxial furrows in Types 1 of *M. decora* (Fig. 10) and *M. rufa* and between the vbs in *M. lupulina* and Types 3 of *M. decora* and *M. rufa*. *Stomata:* low dome-shaped; seldom high-dome-shaped as in Fig. 11; occur in every file of intercostal zones; usually separated by single interstomatal long cell (Figs 16 & 18); interstomatal long cells short to elongated with parallel side walls; slightly undulating; sometimes separated by single short cell. *Papillae:* absent. *Prickles:* none observed. *Micro-hairs:* uncommon; basal cell extremely long; equal to 3× the length of the stomata; distal cells not observed. *Macro-hairs:* absent. *Silica bodies:* uniform in shape; round to slightly vertically elliptical; throughout costal zones; always associated with a narrow cork cell. *Costal zone:* arrangement very uniform; silico-suberose couples always separated by single costal long cell; adjacent files alternate resulting in brickwork pattern. Costal long cells are distinctive in that they are wide and distinct with side walls usually bowed outwards due to the cells being somewhat inflated (Figs 13, 14, 16 & 18); this is not always the case and the side walls may be parallel (Figs 12 & 15). Costal zones are from 7–13 files of cells wide and composition and arrangement is consistent throughout.

Specimens examined:

M. decora

Type 1

CAPE.—3320 (Montagu): Barrydale (–DC), *Ellis 657.* 3321 (Ladismith): Garcias Pass, Riversdale (–CC), *Ellis 2543.*

Type 2

CAPE.—3322 (Oudtshoorn): Robinsons Pass, Outeniqua Mts. (–CC), *Ellis 2549, 2552, 2553.*

Type 3

CAPE.—3322 (Oudtshoorn): George (–CD), *Cook* s.n. Cradocksberg, *Fourcade 4086.*

M. lupulina

CAPE.—3318 (Cape Town): Jonkershoek, Stellenbosch (–DD), *Ellis 2254, 2255, 2256, Taylor 4513, 5477, Van Rensburg 199.*

M. rufa

Type 1

CAPE.—3418 (Simonstown): Cape Point (–AD), *Ellis 2324,* Red Hill, *Taylor 5243.*

Type 2

CAPE.—3318 (Cape Town): Red Hill (–DB), *Taylor 4130.* 3418 (Simonstown): Cape Hangklip (–BD), *Ellis 2517.* 3419 (Caledon): Lebanon (–AA), *Kruger 199.*

Type 3

CAPE.—3118 (van Rhynsdorp): Giftberg (–DC), *Esterhuysen 22128.* 3219 (Wuppertal): Sneeuberg, Clanwilliam (–AC), *Edwards 158;* Buffelberg Pass, Citrusdal (–CA), *Ellis 1190.* 3318 (Cape Town): Kirstenbosch (–CD), *Compton 12014.* 3319 (Worcester): Witzenberg Mts., Ceres (–AC), *Ellis 2483.* 3418 (Simonstown): Hottentots Holland Mts., Sugarloaf Peak (–BB), *Ellis 2298.* 3419 (Caledon): Lebanon (–AA), *Kruger 491.* 3420 (Bredasdorp): Bontebok Nat. Park, Swellendam (–BB), *Liebenberg 6593.*

DISCUSSION AND CONCLUSIONS

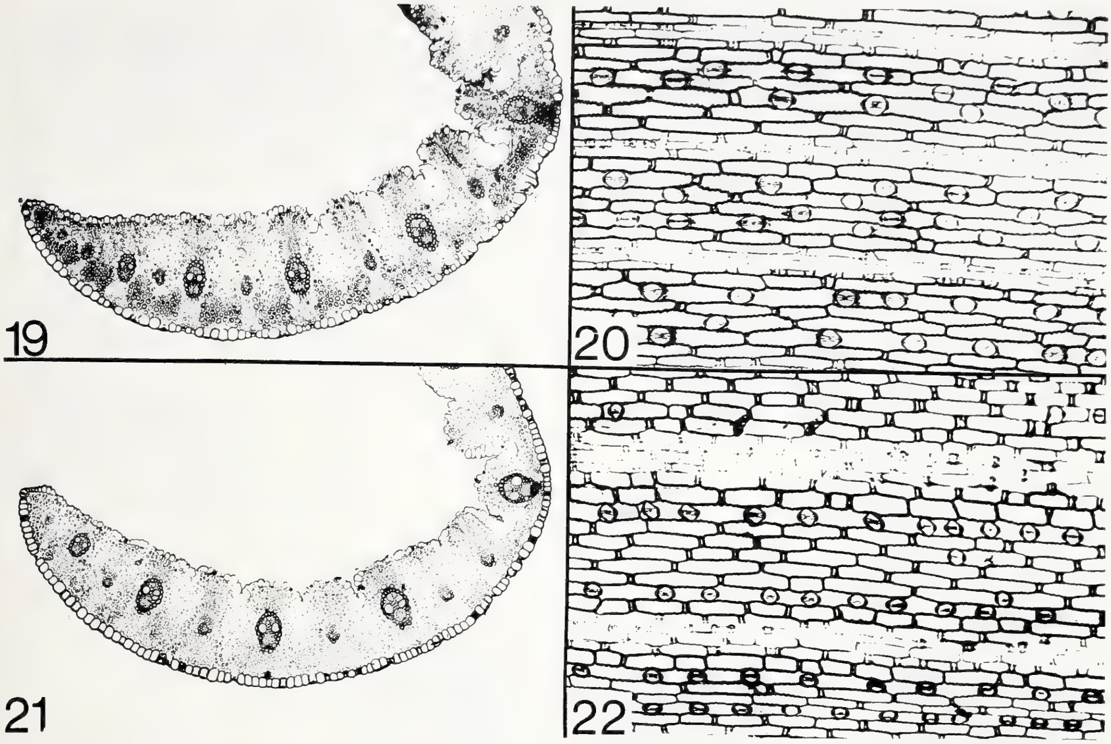
Epidermal structure, particularly of the costal zones, is remarkably consistent throughout the three species studied. All specimens have rounded to elliptical silica bodies which are closely associated with a tall and narrow cork cell. These silico-suberose couples are separated by characteristic costal long cells which have the side walls outwardly bowed. Adjacent files alternate in their arrangement resulting in a brickwork pattern (Figs 10–18). This type of epidermal configuration is unique in the South African danthonoid grasses and differs from all other *Merxmuellera* species. This inflated nature of the costal long cells coupled with the silicose-suberose pairs has also been described in the Drakensberg and Alpine bog farms of *M. disticha* (Nees) Conert (Ellis, 1980). This resemblance is not close, however, and no significance is placed on it. The epidermis of *M. dura* (Ellis, 1982) bears the strongest resemblance with this type.

Morphologically these three species form a distinct group within the genus *Merxmuellera* — their woolly leaf sheaths and expanded bases sunken into the ground being unique in the genus. This close relationship is confirmed by the anatomy, particularly of the epidermis, but this also emphasizes the isolated position within the genus that these species occupy. Epidermal structure, and the cross-sectional anatomy of the majority of the specimens examined, in fact indicates nothing to suggest a close relationship with *Merxmuellera* at all.

The *M. lupulina* type of anatomy (Figs 4–6) is characterized by the leaf not being permanently infolded but involute as well as very little lignin being present in the girders. This structural type occurs in 62% of the 26 specimens examined in this study — all the *M. lupulina* specimens and 2 *M. decora* and 8 *M. rufa* specimens (Type 3 of Fig. 23). Consequently all these specimens bear little resemblance to any *Merxmuellera* species based on leaf anatomy as well as epidermal histology.

This observation is made more significant by the fact that these Type 3 specimens of Fig. 23 show close anatomical resemblances to *Pentaschistis involuta* (Steud.) Adamson and some *P. viscidula* (Nees) Stapf specimens. This is particularly so in the case of the leaf in transverse section (Figs 19 & 21). The epidermis superficially resembles the condition in the *M. lupulina, M. decora & M. rufa* group in that the long cells are inflated and the silica bodies are associated with cork cells. However, closer examination shows that these inflated long cells are actually intercostal cells and not costal cells — the costal zones, although very reduced, being entirely different (Figs 20 & 22). All intermediates do occur between the two extremes, however, and the anatomical indications are, therefore, that the *M. lupulina* type of anatomy has more in common with *P. involuta* than with any of the other *Merxmuellera* species.

This anatomical resemblance is confirmed by the morphology and ecology of these two *Pentaschistis* species. The plant bases are somewhat swollen with persistent leaf sheaths which are sometimes woolly



FIGS 19–22.—Leaf anatomy of *Pentaschistis involuta* and *P. viscidula* for comparative purposes. 19–20, *Pentaschistis involuta, Ellis* 2542: 19, transverse section, × 100; 20, abaxial epidermis, × 160. 21–22, *Pentaschistis viscidula, Ellis* 2554: 21, transverse section, × 100; 22, abaxial epidermis, × 160.

but, nevertheless, usually hairy. *P. involuta* and *P. viscidula* both respond positively to burning and regenerate readily after fire, as do the group of *Merxmuellera* species under discussion. Anatomically *P. involuta* resembles *P. aristidoides* (Thunb.) Stapf more closely than any other *Pentaschistis* species. The similarity is mainly in the leaf anatomy and not the epidermis. It is interesting to note that *P. aristidoides* is the only other *Pentaschistis* with the lowest leaf sheaths woolly or silkily hairy at the base and with swollen bases (Chippindall, 1955).

The anatomy, therefore, suggests that all the *M. lupulina*-like specimens bear a strong link to *P. aristidoides* and that *P. involuta* cannot be satisfactorily separated from *M. lupulina.* This group of species appears to form a link between *Pentaschistis* and *Merxmuellera* and it will be interesting to see whether detailed spikelet comparisons and cytological studies confirm the anatomical indications.

The following *Pentaschistis* specimens bear a strong resemblance to *M. lupulina:*

P. involuta

CAPE.—3418 (Simonstown): Hottentots Holland Mts.; Sir Lowry's Pass (–BB), *Ellis 2284, 2285, 2290, 2291;* Kogelberg (–BD), *Boucher 1194.* 3321 (Ladismith): Garcias Pass, Langeberg (–CC), *Ellis 2542.*

P. viscidula

CAPE.—3320 (Montagu): Tradouws Pass, Barrydale (–DC), *Ellis 658.* 3322 (Oudtshoorn): Robinsons Pass, Outeniqua Mts. (–CC), *Ellis 2554.*

In the *M. decora* sample studied, the two specimens with *M. lupulina*-like anatomy (*Cook* s.n. & *Fourcade* 4086), have actually been examined by Conert and determined as being *M. decora.* The other specimens used in this study, although closely resembling the above two specimens in morphology, and accordingly identified as *M. decora* by the National Herbarium, differ radically in anatomy. Similarly, all the material of *M. rufa* determined by Conert has the *M. lupulina* type of anatomy (Fig. 8). Consequently it is just possible that no specimens which deviate anatomically from the *M. lupulina* type have been thoroughly studied taxonomically. This includes all the specimens listed under Types 1 & 2 for both *M. decora* and *M. rufa* under specimens examined. This may explain why morphological studies have not suggested the same patterns of variation as has this study of the anatomy.

The remaining specimens of both *M. decora* and *M. rufa* (with anatomical Types 1 and 2), which do not exhibit a close anatomical resemblance with *M. lupulina,* appear to confirm the relationship of this group of species with the genus *Merxmuellera.* Type 1, consequently, resembles *M. dura* (Stapf) Conert rather closely in transverse section. Both have alternating first and third order vascular bundles and distinct abaxial furrows (Ellis, 1982). The epidermis of *M. dura* also has distinct silico-suberose couples but lacks the inflated costal long cells. The Type 2 *M. decora* and *M. rufa* specimens either resemble the *M. disticha* (Nees) Conert, or the *M. stricta*

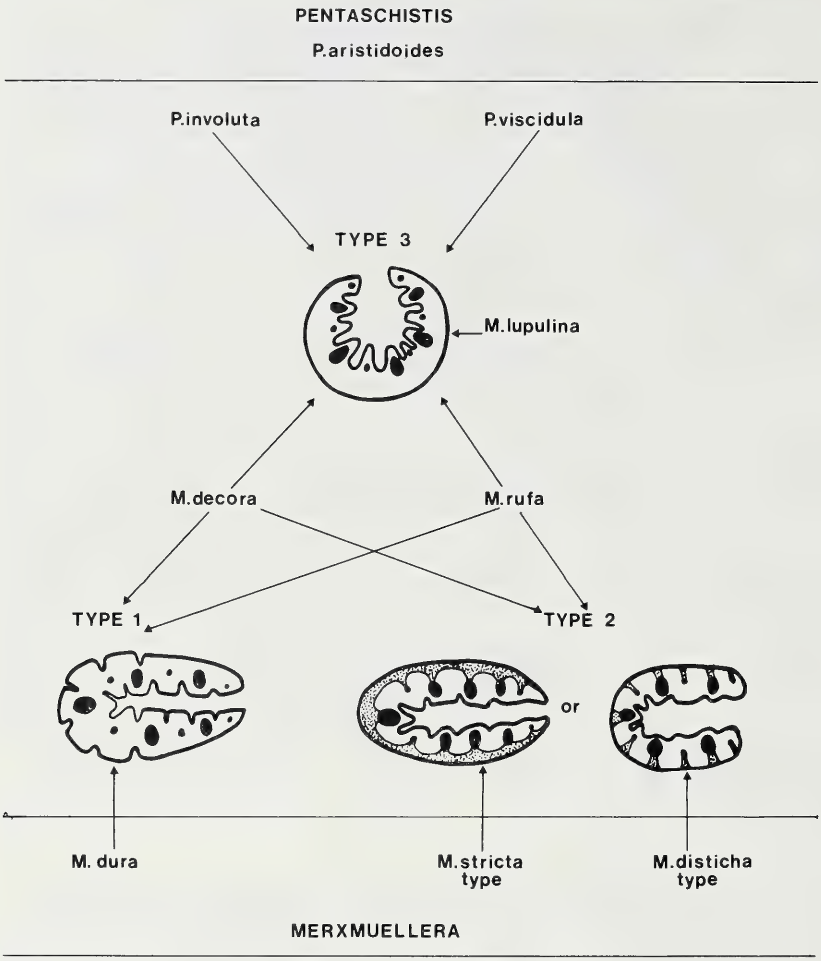


FIG. 23.—Schematic representation of relationships of *Merxmuellera decora, M. lupulina* and *M. rufa* to each other and to the genera *Pentaschistis* and *Merxmuellera.*

(Schrad.) Conert groups (Ellis, 1981). The alternating bundles of different orders of the *M. rufa* specimens of this type resemble the condition in the *M. disticha* group of species whereas the successive lateral first order bundle sequence in the *M. decora* specimens resemble the *M. stricta* type. It is, therefore, possible that these specimens indicate a hybrid origin with *M. stricta* and *M. disticha* (in which group *M. dura* is included).

M. decora, M. lupulina & M. rufa, together with *Pentaschistis involuta,* therefore, appear to form a distinct morphological and anatomical entity intermediate between the genera *Merxmuellera & Pentaschistis.* The taxonomic implications of these anatomical observations appear to be critical to a better understanding of these two danthonoid genera. Either they should all be placed in a new genus intermediate between *Merxmuellera* and *Pentaschistis* and accepted as such or the concept of the genus *Merxmuellera* must be altered. This questions the recognition of the genus *Merxmuellera* and raises the possibility of a reacceptance of the genus *Danthonia.* Careful morphological analyses are urgently required to resolve this question. Finally, this study has revealed that neither *M. decora* or *M. rufa* are homogeneous entities as presently constituted and it appears that a more satisfactory arrangement would be the grouping of all Type 1 specimens in one of these taxa and all Type 2 specimens in the other.

ACKNOWLEDGEMENTS

Dr B. de Winter, Mr P. C. V. du Toit and Miss L. Smook kindly identified the voucher specimens and Mrs A. Romanowski assisted with the photography. Miss H. Botha prepared the table.

UITTREKSEL

Die blaaranatomie van Merxmuellera decora *(Nees) Conert,* M. lupulina *(Thunb.) Conert en* M. rufa *(Nees) Conert word beskryf en geïllustreer. Dit is bewys dat die epidermisstruktuur in al drie spesies eenders is en dat dié struktuur uniek in die genus is. Die blaaranatomie varieer baie en drie verskillende soorte is duidelik. Die anatomie van* M. lupulina *is deurgaans konsekwent maar al drie anatomiese soorte is teenwoordig in die ondersoekte monsters van beide* M. decora *en* M. rufa. *Die anatomiese soorte*

toon ooreenkomste met Pentaschistis involuta *(Steud.) Adamson,* M. dura *(Stapf) Conert,* M. stricta *(Schrad.) Conert en* M. disticha *(Nees) Conert. Dit blyk dus dat,* M. decora, M. lupulina *en* M. rufa, *tesame met* P. involuta, *'n duidelik erkenbare groep vorm wat intermediêr tussen* Pentaschistis *en* Merxmuellera *ressorteer.*

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Bothalia 14, 2: 205–213 (1983)

The taxonomic position of C_3 and C_4 *Alloteropsis semialata* (Poaceae) in southern Africa

G.E. GIBBS RUSSELL*

ABSTRACT

Alloteropsis semialata (R. Br.) Hitchc. sensu Chippindall (1955) and Clayton (in press) is the only known grass species in which elements with both non-Kranz and Kranz leaf blade anatomy, and therefore with C_3 and C_4 photosynthetic pathways are included. In the past, two taxa had been recognized, but the characters used to separate them were found to be unreliable, so they were united. However, study of voucher specimens for anatomical and physiological work has shown that C_3 and C_4 taxa may be separated on the basis of morphological characters that differ from those considered in the past. Therefore, two taxa are again recognized, this time at the rank of subspecies, and the name *Alloteropsis semialata* subsp. **eckloniana** (Nees) Gibbs Russell *stat. nov.* is published.

INTRODUCTION

Alloteropsis semialata (R. Br.) Hitch. is a grass of common, though never dominant, occurrence in the grasslands and open woodlands of the eastern part of southern Africa. Acocks (1975) reports it as an important constituent of 13 veld types. Its worldwide distribution extends from southern and tropical Africa to India, China, the Philippines and Australia.

Ellis (1974a, 1974b) has shown that the species as accepted by Chippindall (1955) and Clayton (in press) has both non-Kranz and Kranz leaf anatomy, and therefore has C_3 and C_4 photosynthetic metabolism. Frean & Cresswell (1979), Frean, Barrett & Cresswell (1980) and Ellis (1981) report the physiological features of C_3 and C_4 individuals in details and give additional differences in plant morphology and epidermal anatomy.

A. semialata is the only known grass which has both C_3 and C_4 metabolic forms. In the Poaceae, either pathway is normally characteristic at the taxonomic levels of subfamily and tribe, but two subfamilies, the Panicoideae and Arundinoideae, have both pathways. All the genera in Paniceae (*s.l.*) are either C_3 or C_4 except *Panicum, Neurachne* and *Alloteropsis,* but within *Panicum* and *Neurachne* (Hattersley, Watson & Johnson, 1982) individual species are either C_3 or C_4. In *Alloteropsis* alone is there a species recognized that exhibits both anatomical types and both physiological processes (Ellis, 1974a).

The aim of this paper is to show that the C_3 and C_4 anatomical/physiological forms are supported by vegetative characters that do not intergrade in southern Africa, and which differ from characters used previously to separate entities in the species. The two forms are recognized as subspecies.

HISTORICAL BACKGROUND

In the past, two entities which are currently combined in *A. semialata* (R. Br.) Hitchc. have been recognized, one with long racemes with loosely-placed, pale spikelets, and the other with short racemes with tightly-packed, very dark spikelets. The variants and the intergradation between them have been treated in several ways in the past.

Nees was the first to deal with both entities. In 1833 he created a new genus, *Coridochloa*, and transferred to it *Panicum semialatum* R. Br., which had been described by Robert Brown in 1810 on the basis of a specimen from Carpentaria in Australia. In 1834, Nees described a new monotypic genus *Bluffia eckloniana*, based on specimens collected by Drège at Katberg and Port Natal. Nees therefore considered that the two entities belonged to different genera.

By the end of the century, the taxa were better known over their large range, and they were seen to be more closely related. Hackel (1894) reduced *Bluffia eckloniana* to a variety of *Panicum semialatum.* Two years later, working on specimens from India, Hooker (1896) moved *Panicum semialatum* to the genus *Axonopus.* Stapf (1899) in *Flora Capensis* followed the generic placement of Hooker and the varietal placement of Hackel, and called the South African plants *Axonopus semialatus* (R. Br.) Hook. f. var. *ecklonii* Stapf, but treated the variety name as 'new'.

The current generic placement of the taxa was effected by Hitchcock (1909) when he recognized that the type specimen of Presl's (1830) genus and species *Alloteropsis distachya* was identical to *Panicum semialata* (Nees) Hitchc. (Chase, 1911). He did not at that time transfer Nees's southern African entity to the new genus, but in 1916 published the new combination *A. eckloniana* (Nees) Hitchc., therefore evaluating the differences between the two taxa at the specific level.

Stapf (1919) in Flora of Tropical Africa followed Hitchcock's acceptance of Presl's genus, but again treated the southern African taxon as a variety, *A. semialata* (R. Br.) Hitchc. var. *ecklonii* (Stapf) Stapf, once more using his own epithet '*ecklonii*'.

More recently, variation within the species has not been given taxonomic status. Phillips used only the name *A. semialata* and did not recognize a variety. Chippindall (1955) stated specifically that

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the variety (*'ecklonii'*) should be disregarded because the range of variation was so wide that the characters were not diagnostic. Clayton (in press) has adopted the same course for the Flora of Tropical East Africa. He says that the southern African variety is of limited taxonomic significance, because it merges completely with the rest of the species. He mentions the anatomical differences found by Ellis (1974a, 1974b), but does not comment on their taxonomic value.

During this long history of changes in interpretation, the two have been treated as different genera, different species and different varieties. They have most recently been reduced to a single variable species, when it became clear that the 'Australian' form also occurred in southern Africa, and that the criteria originally used to separate the taxa, mainly raceme colour, density and length, were variable and did not serve to separate the taxa adequately. An unfortunate result was that when anatomical and physiological investigations showed great differences within the species, there was no way to deal with the differences taxonomically at that time, because the infraspecific taxa had already been rejected on other grounds.

SEPARATION OF THE TAXA USING ANATOMICAL AND VEGETATIVE CHARACTERS

Re-evaluation of the variation within *A. semialata,* taking into account the anatomical differences that are indicators of different pathways, was possible because Ellis made over 50 voucher specimens for which determination of C_3 (non-Kranz) or C_4 (Kranz) anatomy had been carried out. These specimens were scored for a number of characters: length of longest raceme, spikelet colour, shape of leaf tip, width of leaf blade, hairiness of leaf blade, outline shape of basal parts, width of veins in basal sheath, length of hairs on basal sheath, and splitting of basal sheath into fibres. Fig. 1 shows the characters finally used to illustrate variation between the forms. The first analysis of this data showed that Chippindall and Clayton were correct in discounting raceme length and spikelet colour as valid characters to separate taxa. They did indeed often (but not always) vary independently from each other. However, two vegetative characters were found that consistently separated the C_3 and C_4 forms. These were width of veins in the basal sheath and width of leaf blade 20 mm from the tip (measuring the broadest basal leaf). Fig. 2 shows the scatter diagram produced with these characters on the x- and the y- axis. The two anatomical/physiological forms are separated, on both axes.

It is evident from this diagram that even though short racemes, dark spikelet colour and very hairy leaf blades are often associated with the C_3 form, C_3 plants may occasionally have long racemes, pale spikelet colour and glabrous leaf blades. Conversely, C_4 plants usually have long racemes, pale spikelets and glabrous leaf blades, but they may also have any combination of characters at the other extreme. Intermediate states of these characters can occur in either anatomical form. However, the two forms can always be distinguished by a combination of the

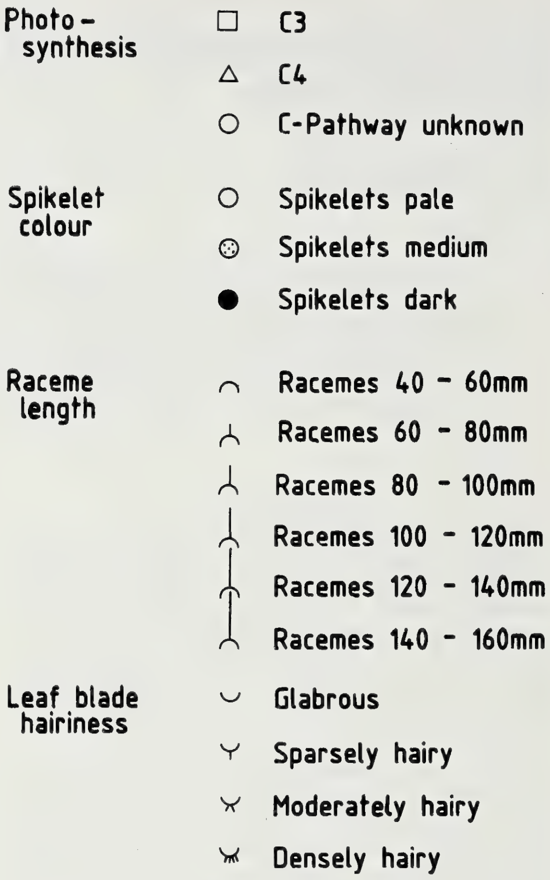

FIG. 1. — Character states shown in the scatter diagrams (Figs 2, 3 and 4).

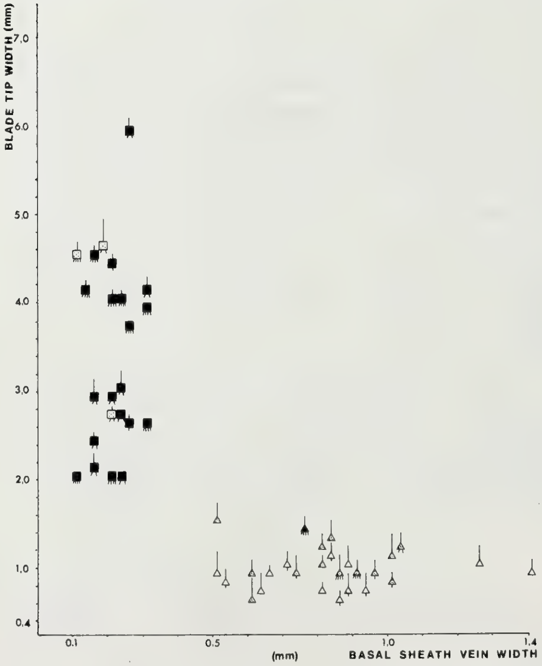

FIG. 2. — Specimens from southern Africa of known C_3 / C_4 state in R.P. Ellis's collection of voucher specimens for anatomical study. (Specimens are listed individually in the systematic treatment of each subspecies.)

width of the veins in the basal sheath and the width of the leaf blade 20 mm from the tip.

Fig. 3 shows a pattern similar to that for Fig. 2 when all the PRE specimens from southern Africa of which the anatomy had not been determined were plotted using the same characters. Again, there is a separation into two groups on the basis of width of veins in the basal sheath and width of the leaf blade near the tip. The similarity of the pattern formed by these specimens, for which the anatomical state is not known, to the pattern formed by Ellis's voucher specimens examined for C_3 or C_4 anatomy, makes it possible to predict the anatomical state. Specimens with narrow veins in the basal sheath and broad leaf tips have C_3 leaf anatomy, and specimens with broad veins in the basal sheath and narrow leaf tips have C_4 anatomy. The characters of short dense dark racemes and markedly hairy leaf blades are often correlated with the C_3 form, and the characters of long loose pale racemes and glabrous leaf blades are often correlated with the C_4 form. However, intermediates and even sometimes the extreme states for these characters can occur in either anatomical form. An interesting sub-group of the C_3 plants with exceptionally broad leaf tips (wider than 4,6 mm) and with a medium-brown spikelet colour, occurs in southern Natal, Transkei and the eastern Cape.

It is worth noting that the specimens of Ellis do not show any C_3 plants with leaf tips narrower than 2,0 mm, but that there are a number with apparently narrower tips among the herbarium specimens plotted. This is probably an artefact of collection. In specimens which are not immediately pressed, the leaf blades roll considerably, and therefore appear narrower than in the case of Ellis's well-prepared specimens.

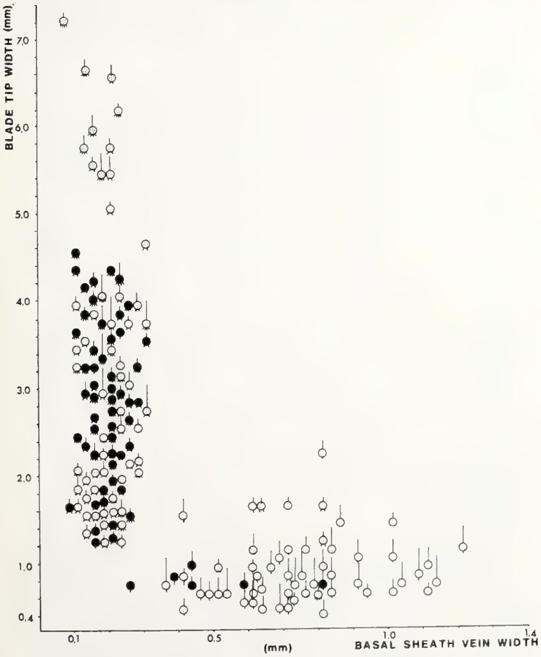

FIG. 3. — Specimens from southern Africa of unknown C_3 / C_4 state, in the herbarium collection at PRE. (Specimens are listed individually in the systematic treatment of each subspecies.)

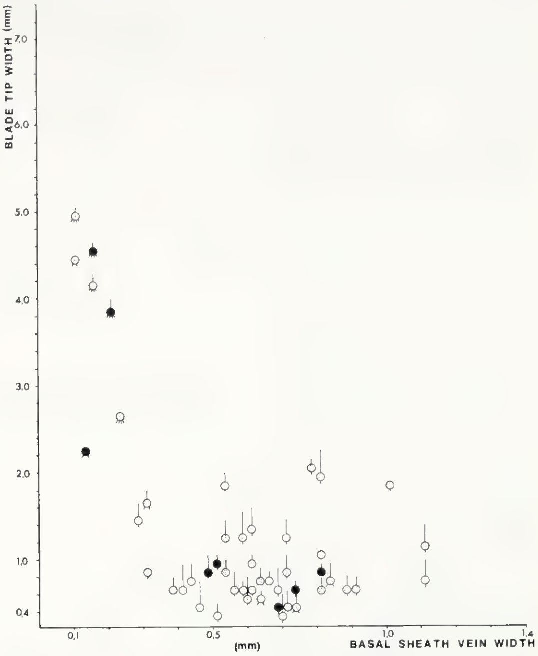

FIG. 4. — Specimens from tropical Africa of unknown C_3 / C_4 state, in the herbarium collection at PRE.

Specimens at PRE from tropical Africa that have not been examined anatomically are shown in Fig. 4. Again, there is separation into two groups on the basis of width of veins in the basal sheath and width of leaf blade tip. All the specimens in the C_3 group are from the eastern highlands of Zimbabwe except one from Tanzania collected at an altitude of 1830 m. Ellis (1981) has pointed out that in southern Africa, the C_3 form occupies habitats of higher elevation than the C_4 form. It occurs at the lowest elevations in the Cape and Natal, rising to the central highveld, and in the eastern and northern Transvaal occurring in the Transvaal Drakensberg and in the Soutpansberg. This increase in altitude with decreasing latitude for C_3 plants is therefore borne out by the data from tropical Africa.

MORPHOLOGY

Both the subspecies are robust perennial tufted grasses, with short stout deeply buried rhizomes. The basal portions of the sheath and culms are usually buried to a depth 50–100 mm. The shape in outline of the buried parts is often different in the two subspecies. I subsp. *semialata* (the C_4 form), the lowest portion above the rhizome is often expanded and somewhat bulbous, with the upper section a bit narrower and parallel-sided, whereas in subsp. *eckloniana* (the C_3 form) the lowest portion is not bulbous and the sheaths spread slightly outwards from each other so that the outline is V-shaped. The basal sheaths of both subspecies are usually extremely hairy, with the hairs arising between the veins. The veins of subsp. *semialata* are very wide, and appear as broad yellowish ribs, with the hairs emerging between them. The veins of subsp.

TABLE 1. — Anatomical and physiological features of the subspecies of *A. semialata*

Character	C_3 form (subsp. *eckloniana*)	C_4 form (subsp. *semialata*)
Leaf blade anatomy (Ellis, 1974a)		
Inner vascular bundle sheath	Mestome sheath of small thickened cells	Parenchyma sheath with inflated cells containing large chloroplasts.
Outer vascular bundle sheath	Parenchyma sheath of large thickened cells with no or few unspecialized chloroplasts.	Thin-walled cells smaller than cells of inner v.b. sheath, with no or few chloroplasts similar to mesophyll chloroplasts.
Chlorenchyma cells	Tabular, indistinctly radiate with larger intercellular air spaces	Larger than v.b. sheath cells, hexagonal to inflated, with small intercellular air spaces.
Leaf surface (Frean *et al.*, 1980)		
(adaxial surface of leaf 2)		
Area	1 138	674
No. stomata/mm^2	181	70
No. stomata/leaf	206 350	47 180
Ave. area of stomata in 1 mm^2	$1,54 \times 10^{-4}$	$3,30 \times 10^{-4}$
% stomatal area	2,80	2,31
No. epidermal cells/mm^2	1 450	540
Stomatal index	11,2	9,3
Resistance to desiccation (Ellis, 1981)	by concertina pleating	by rolling
Epidermal macrohairs (Frean & Cresswell, 1979)	present	usually absent
Wax crystals	absent	present
Physiology (Frean *et al.*, (1980)		
($\overline{X}$ of plants examined)		
Average photosynthesis (ng / cm^2 / s)	21	33
Average transpiration (ug / cm^2 / s)	1,60	0,65
Transpiration/photosynthesis ratio	76,5	19,0
Leaf resistance to water loss (Ellis, 1981, reporting B.N. Smith & J. Vogel)	8,5	15,5
Carbon isotope ratios (Ellis, 1981, reporting J. Vogel, unpublished)	−25,2– −28,5	−9,3– −13,8
CO_2 compensation point	50 ppm	5 ppm
Cytogenetics (Ellis, 1981, reporting W.V. Brown & C. Hsu)		
2n chromosome number	18	18, 36, 54

eckloniana are much narrower and the broad spaces between them are covered with hairs. The hairs in both species are usually so long that the veins are often difficult to see unless some of the hairs are scraped away. A difference between the subspecies that is probably a result of the differences in the veins of the basal sheaths is the tendency of the old sheaths to split into fibres. In subspecies *eckloniana* often the basal sheaths split into fine fibres from the top. In subsp. *semialata* this does not happen, although the thickened veins may sometimes separate at the base where they curve around to the rhizome.

Leaf blade differences useful in separating the subspecies can sometimes be observed in living plants. Frean *et al.* (1980) report that the leaf blades of the C_3 plants are held erect, and the leaf blades of the C_4 plants droop downwards from the middle. The C_3 plants also usually hold their leaf blades flat, whereas the C_4 plants hold their leaf blades slightly curved upwards at the edges. However, although these characters can be useful in the field for quick identification, they are not always reliable, especially in places that have been recently burned. Perhaps for this reason, specimens from the Ermelo area are particularly difficult to place in a subspecies on the basis of their leaves. As shown by the scatter diagrams, subsp. *ecklonian*a tends to have more hairy leaf blades than subsp. *semialata*, but individuals in each taxon may vary greatly in this respect.

The inflorescence characters of raceme length, density of spikelets on the axes, and spikelet colour are the traditional ones used to separate the two variants but, as has been discussed above, they are not constant and are therefore unreliable.

No spikelet character has been found to separate the subspecies. Subspecies *semialata* tends to have longer spikelets and those of subsp. *eckloniana* tend to be shorter, but there is a great overlap between them in the middle of the range. Other spikelet characteristics, such as nervation and outline, are similar in both subspecies, whereas vesture and degree of winging of the upper glume appear to vary randomly in both subspecies.

ANATOMY AND PHYSIOLOGY

Differences in leaf blade anatomy and physiological differences related to the different photosynthetic pathways for the two subspecies have been reported by a number of authors since the first reports of the unusual condition of *A. semialata* by Ellis (1974a). These reports are summarized in Table 1. The marked differences shown by the C_3 and C_4 forms in a large number of characteristics warrants taxonomic recognition, especially when supported by discernable morphological differences.

DISTRIBUTION AND ECOLOGY

Distribution maps for the two subspecies in southern Africa are given in Figs 5 & 6. Subspecies *eckloniana* extends as far south as the eastern Cape, but *semialata* reaches only to Natal. The ranges of the two taxa overlap for most of the country, but in many of the areas, Ellis (1981) has shown that the C_3 plants grow at higher altitude than the C_4 plants. These patterns agree with the findings of Vogel, Fuls & Ellis (1978), where it is demonstrated that C_3 plants are favoured by higher temperatures. The distribution of both subspecies in South Africa corresponds closely with the area indicated by Vogel *et al.* (1978) as predominantly composed of C_4 grass species (75–95% are C_4).

Ellis (1981) also presents the results of soil analysis which show that in the Transvaal Bankenveld the C_3 form grows on moderately to strongly acid soils, and the C_4 form prefers soils that are only slightly acid. This suggests that the taxa may be kept separate by adaptation to different edaphic conditions, as discussed by Gentry (1980).

In a number of localities near Pretoria, Johannesburg and Middelburg in the Transvaal and Eston and Estcourt in Natal, (Ellis, 1981 and pers. comm.) populations of both sub species grow in close proximity, within 100 metres of each other. Even here, no intermediates have been found, either in leaf anatomy, C_{12}/C_{13} ratios, CO_2 compensation point, or in the vegetative characters which indicate the leaf blade anatomy. This indicates that no hybridization has occurred in nature between the two taxa in southern Africa, and is an additional reason for recognizing them as separate entities.

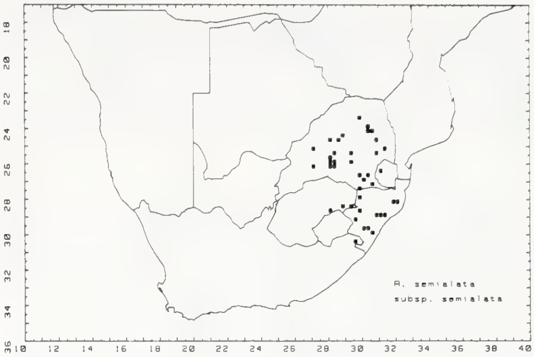

FIG. 5. — Distribution of *Alloteropsis semialata* subsp. *semialata* in southern Africa.

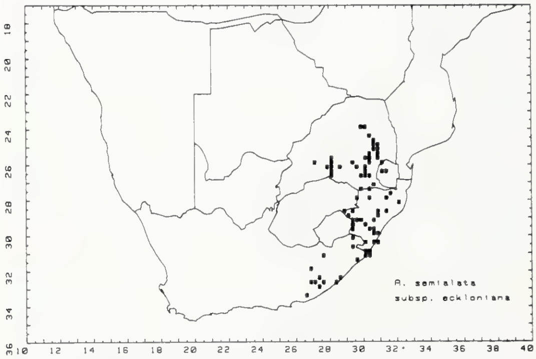

FIG. 6. — Distribution of *Alloteropsis semialata* subsp. *eckloniana* in southern Africa.

TAXONOMIC TREATMENT

1. **Alloteropsis semialata** (R. Br.) Hitchc. in Contrib. U.S. Nat. Herb. 12: 210 (1909); F.T.A. 9: 483 (1919); Chippind. in Meredith, Grasses & Pastures S. Afr. 423 (1955); Gordon-Gray in Ross, Fl. Natal 80 (1972). Type: Australia, Carpentaria, *Brown* 6101 (K, iso.!; BM, holo!).

Panicum semialatum R. Br., Prodr. 192 (1810). *Urochloa semialata* (R. Br.) Kunth, Rev. Gram. 1: 31 (1829). *Oplismenus semialatus* (R. Br.) Desv., Opusc. 81 (1831). *Coridochloa semialata* (R. Br.) Nees in Edib. New Phil. 15: 381 (1833). *Axonopus semialatus* (R. Br.) Hook. f. in Fl. Brit. India 7: 64 (1896). *Paspalum semialatum (R. Br.) Eyles in Trans. Roy. Soc. S. Afr. 5: 299 (1916).*

This species is the only known grass with Kranz type leaf anatomy and C_4 carbon metabolism as well as non-Kranz leaf anatomy and C_3 carbon metabolism. These two forms are recognized as subspecies.

Leaf blades rolled or curved upwards, tapering gradually to tip, sparsely hairy, linear, hard-textured; veins on old leaf sheaths at base of culms forming ribs 0,5–1,1 mm across; racemes often (but not always) longer than 80 mm with light coloured spikelets loosely arranged .... (a) *A. semialata* subsp. *semialata*

Leaf blades flat, tapering abruptly to tip, usually densely hairy; lanceolate, ± soft-textured; veins on old leaf sheaths at base of culms to 0,3 mm across; racemes often (but not always) shorter than 80 mm with dark coloured spikelets tightly packed together..(b) *A. semialata* subsp. *eckloniana*

(a) subsp. **semialata**

Tufted perennial with short stout creeping rhizomes; *basal parts* with old sheaths tightly appressed into a stout bulbous base, parallel sided or ovoid in outline, with very dense hairs to 4 mm long, not splitting into fibres, (rarely splitting from bottom), veins forming broad flat ribs to 0,5–1,1 mm across; *culms* erect, 300–1300 (–1500) mm tall, nodes woolly, internodes sparsely scabrous to glabrous, base stout, clad in old leaf sheaths. *Leaf* blades linear, 3–5 (–6) mm wide, usually curved upwards or loosely rolled, tapering gradually to tip, sparsely hairy. *Inflorescence* of 2–6 digitate racemes 30–220 mm long, sometimes bare near base. *Spikelets* 5–8 mm long (excluding mucros and awns), tan, brown, or purple, sometimes with dark transverse bars; upper glume abruptly ending in a mucro to 3 mm long, sometimes with marginal flaps; lemmas usually both with awns to 3 mm long. *Anatomy* of leaf blades is Kranz-type. *Carbon metabolism* is C_4. (Fig. 7.)

Natal and Zululand north through the eastern Orange Free State and Swaziland to the Transvaal; also occurring through eastern, central and west tropical Africa to India, south-east Asia, Malaysia, and northern and eastern Australia. Grows in grasslands, rocky hillsides and bushveld woodland, usually at lower altitudes and in less acid soils than the other subspecies.

TRANSVAAL. — 2330 (Tzaneen): Duiwelskloof (–CA), *Scheepers 776*. Valencia (–CD), *Rinder 8*. 2428 (Nylstroom): Vaalwater (–AB), *Codd 922*. 2430 (Pilgrim's Rest): Mariepskop (–DB), *Van der Schijff 6152*. 2527 (Rustenburg): Pilanesberg (–AA), *Pole Evans 631; Smook 958,* 1019. 2528 (Pretoria): Kwandebele (–BD), *Smook 3160;* Pretoria Dist. (–CA), *De Winter 8645; Rietondale* (–CA), *Chippindall 112;* Nat. Botanic Garden (–CA), *Crook 2056;* Meintjies Kop (–CA), *Fouche* (PRE) *7648;* Elofsdal (–CA), *Hanekom 1696;* Nature Reserve (–CA), *Kok 237;* Pretoria (–CA), *Leendertz TM 6221;* Pretoria Dist. (–CA), *MacDonald PRE 285;* Sunnyside Hill (–CA), *Mogg 15987;* Wonderboom Station (–CA), *Phillips 3516*; Rietfontein (–CA), *Pole Evans 277*; Waterval (–CA), *Pole Evans 1523;* Fountains Valley (–CA), *Skead 57;* Waterkloof (–CA), *Verdoorn 74;* Pretoria (–CA), *Wager TM 14655;* Doornhoogte, Irene (–CC), *Pole Evans 509;* Lyttelton Station (–CC); *Pole Evans 511;* Faerie Glen (–CD), *Group 1 1;* Faerie Glen (–CD), *Group 2 67;* Faerie Glen (–CD), *Group 4 37*. 2529 (Witbank): Loskop Dam Nature Reserve (–AD), *Pettifer 706;* Robbertsloop (–AD), *Theron 1237;* Loskop Dam Nature Reserve (–CB), *Theron 1*. 2530 (Lydenburg): Lowveld Botanical Garden (–BD), *Van Jaarsveld 168*. 3531 (Komatipoort): Pretoriuskop, K.N.P. (–AB), *Van der Schijff 3374*. 2627 (Potchefstroom): Goedgedacht (–AA), *Sutton 496*. 2628 (Johannesburg): Modderfontein (–AA), *Haagner TM 3781;* Benoni (–AB), *Bradfield 244;* Benoni (–AB), *Bradfield 272;* Springs (–AB), *Pretoria PRE 33955;* Klipriviersberg, (–AC), *Cohen 698;* 23 km SE of Greylingstad (–DD), *Acocks 12556*. 2629 (Bethal): Standerton Dist. (–CC), *Burtt Davy 3082;* Standerton Dist. (–CD), *Burtt Davy 1020;* Ermelo Dist. (–DA), *Burrt Davy 946;* Ermelo Dist. (–DA), *Collins TM 12203, Collins TM 13450;* Nooitgedacht (–DB), *Henrici 1201;* Nooitgedacht (–DB), *Henrici 1206;* Nooitgedacht (–DB), *Henrici 1285;* Ermelo Dist. (–DB), *Tennant PRE 289*. 2630 (Carolina): Athole Pasture Research Station (–CB), *Norval 83;* Athole Pasture Research Station (–CB), *Norval 119*.

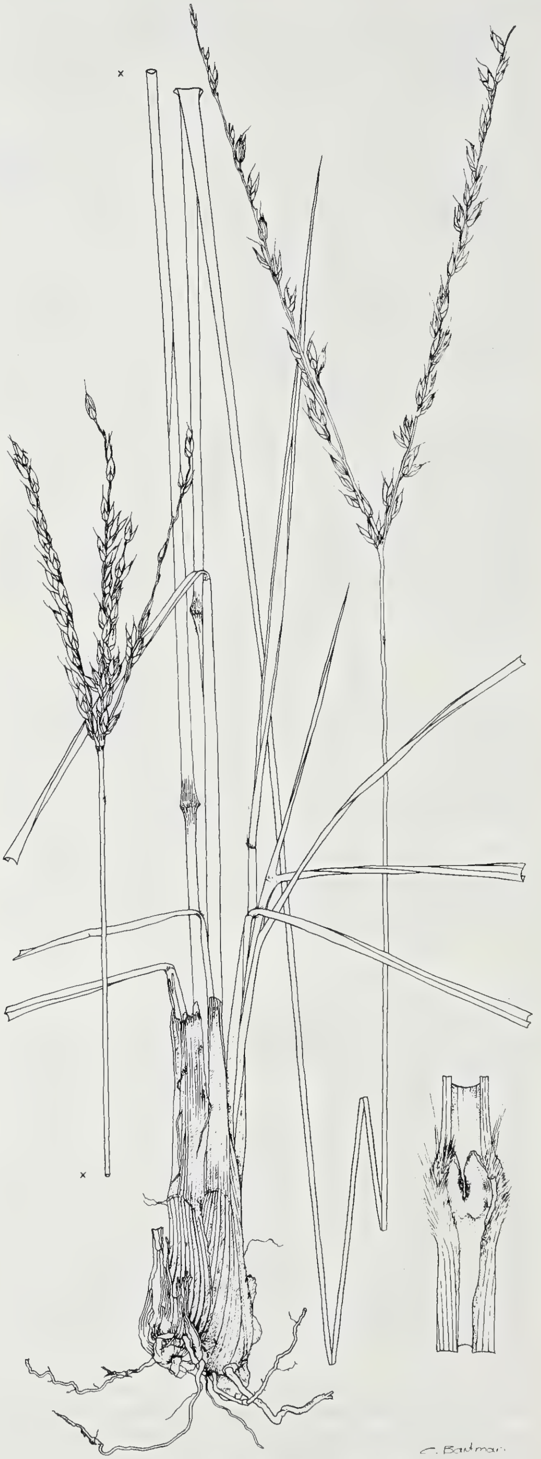

FIG. 7. — Habit of *Alloteropsis semialata* subsp. *semialata*.

SWAZILAND. — 2631 (Mbabane): Mlilwane Wildlife Sanctuary (–AC), *Stephen 1421;* Tshaneni (–BB), *Barrett 209*.

NATAL. — (Harrismith): Slopes of Dooley (–CC), *Doidge PRE 33928*. 2830 (Dundee): Kranskop (–DD), *Stirton 5224*. 2831 (Nkandla): Corridor between Hluhluwe and Umfolozi (–BB), *Hitchins 665;* Corridor between Hluhluwe and Umfolozi (–BB), *Hitchins 716;* Umhlatuzi Lake (–CC), *Venter 3872;* Hluhluwe

Game Reserve (−CD), *Bourquin 640;* Eshowe (−CD), *Halse 59.* 3832 (Mtubatuba): Hluhluwe Game Reserve (−AA), *Hitchins 537.* 2929 (Underberg): Ntabamhlope (−BA), *Miller 349.* 2930 (Pietermaritzburg): Oribi (−CA), *Lawson 591;* Pietermaritzburg (−CB), *Goossens 152.*

C_4 Vouchers

TRANSVAAL. — 2329 (Pietersburg): 13 km from Bandolierkop (−BD), *Ellis 3482;* 17 km from Soekmekaar (−BD), *Ellis 3483, 3484.* 2330 (Tzaneen): 15 km from Tzaneen (−CD), *Ellis 3486.* 2428 (Nylstroom): Doorndraai Dam Nature Reserve (−BD), *Ellis 3497;* Kranskop, Nylstroom Dist. (−CA), *Ellis 3506;* 5 km from Naboomspruit (−DA), *Ellis 3815.* 2430 (Pilgrim's Rest): 2 km from Ofcolaco (−AB), *Ellis 2809;* 35 km from Tzaneen (−BA), *Ellis 3813.* 2528 (Pretoria): Nasionale Botaniese Tuin (−CA), *Manders 9.* 2529 (Witbank): 3 km north of Middelburg (−CD), *Ellis 2832, 2833;* 2 km from Middelburg (−CD), *Ellis 3810.* 2629 (Bethal): 8 km from Ermelo (−DB), *Ellis 3527, 3528, 3807;* 28 km from Ermelo (−DB), *Ellis 3808.* 2630 (Carolina): 35 km from Ermelo (−CC), *Ellis 3530.* 2730 (Vryheid): Kwamandlangampisi Mts (−BA), *Ellis 3532, 3534.*

O.F.S. — 2727 (Kroonstad): Heilbron (−BD), *Brandmuller 47.* 2828 (Bethlehem): Witsieshoek Dist. (−BD), *Ellis 1938.*

NATAL. — 2729 (Volksrust): Majuba Pass (−BD), *Ellis 3769;* 25 km from Newcastle (−DD), *Ellis 3770.* 2829 (Harrismith): Van Reenen's Pass (−AD), *Ellis 3805;* 17 km from Ladysmith (−DB), *Ellis 3771.* 3832 (Mtubatuba): 19 km south of Mtubatuba (−AC), *Strey 5615.* 2930 (Pietermaritzburg): Eston (−DC), *Ellis 3775.*

(b) subsp. **eckloniana** *(Nees) Gibbs Russell,* stat. nov.

Bluffia eckloniana Nees in Lehm., Ind. Sem. Hort. Hamb. 1834 8 (1834), Fl. Afr. Austr. 61 (1841). *Panicum semialatum* R. Br. var. *ecklonianum* (Nees) Dur. & Schinz, Consp. Fl. Afr. 5: 764 (1894). *Axonopus semialatus* (R. Br.) Hook f. var. *ecklonii* Stapf in Fl. Cap. 7: 418 (1899), nom. superfl., based on *Bluffia eckloniana* Nees. *Axonopus ecklonianus* (Nees) Chiov. in Ann. Bot. Roma 13: 47 (1914). *Alloteropsis eckloniana* (Nees) Hitchc. in Proc. Biol. Soc. Wash. 29: 128 (1916). *Paspalum semialatum* (R. Br.) Eyles var. *ecklonii* (Stapf) Eyles in Trans. Roy. Soc. S. Afr. 5: 299 (1916), nom. superfl. *Alloteropsis semialata* (R. Br.) Hitchc. var *ecklonii* (Stapf) Stapf in F.T.A. 9: 485 (1919), nom. superfl. *Axonopus semialatus* (R. Br.) Hook. f. var. *ecklonianus* (Nees) Peter in F.D.O. −A. 1: 165 (1929). *Alloteropsis semialata* (R. Br.) *Hitchc.* var. *eckloniana* (Nees) C.E. Hubb. In Bor, Grasses Burma, Ceylon, India, Pakistan 277 (1960). Isotypes: Katberg, *Drège* (S; K!, isosyn; fragment in PRE!), Port Natal, *Drège* (S, isosyn.).

Similar to the typical subspecies in spikelet structure, but differing in vegetative morphology and often in inflorescence size and colour. *Basal parts* with sheaths usually somewhat separated, base V-shaped in outline, not bulbous, with dense hairs less than 3 mm long, often splitting into fibres from top or middle, veins to 0,3 mm across. *Culms* 250−1100 mm tall, nodes woolly to velutinous, internodes velutinous to glabrous. *Leaf* blades linear-lanceolate, flat, 3−12 mm wide, tapering abruptly to tip, velutinous (rarely only sparsely hairy). *Inflorescence* of 3−7 (−9) racemes 25−90 (−120) mm long, frequently with 1 or 2 racemes branching lower than others which are digitate. *Spikelets* usually dark brown or purplish black, sometimes lighter or barred. *Anatomy* of leaf blades is non-Krantz type. *Carbon metabolism* is C_3. (Fig. 8.)

Eastern Cape northward through Natal to the eastern Orange Free State and the Transvaal; occurring as far north at the eastern highlands of Zimbabwe and mountainous regions of Tanzania. Grows in grassland, on mountain and hillsides often in rocky places, and on forest margins, usually at higher altitudes and in more acid soils than the typical subspecies.

TRANSVAAL. — 2329 (Pietersburg): Haenertsburg (−DD), *Acocks & Hafstrom 60;* Magoebaskloof, (−DD), *Crawford 286;* Haenertsburg (−DD), *Davidse & Loxton 5813;* Iron Crown Mt

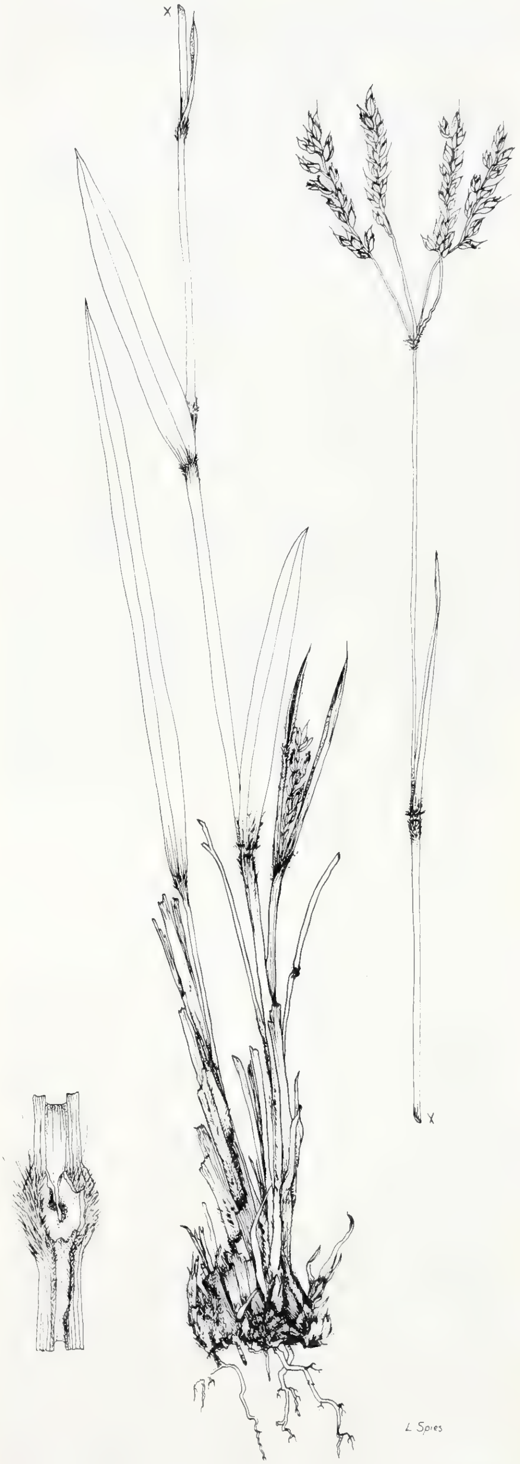

FIG. 8. — Habit of *Alloteropsis semialata* subsp. *eckloniana.*

(−DD), *Mogg 16640.* 2330 (Tzaneen); Grootbosch Forest Reserve, Duiwelskloof (−CA), *Scheepers 835;* New Agatha Forest (−CC), *Muller & Scheepers 217;* Woodbush (−CC), *Wager TM 12518.* 2430 (Pilgrim's Rest); Ohrigstad Nature Reserve (−DA), *Jacobsen 1293;* Dam (−DC), *Jacobsen 2271;* Mac Mac Nature Reserve (−DD), *Kluge 1926.* 2527 (Rustenburg): Derby Station (−CC), *Burtt Davy 7170;* 2528 (Pretoria): Waterkloof (−CA), *Mogg 15049;* Groenkloof (−CC), *Pentz PRE 33973.* 2530 (Lydenburg): Schoemanskloof (−AD), *Smuts 261;* Long Tom Pass (−BA), *Du Toit 1037;* Klipbankspruit (−BA), *Du Toit 1047;* Hartebeestvlakte (−BA), *Mohle 30;* Mauchberg (−BB), *Smuts & Gillett 2300;* Witklip (−BD), *Kluge 204;* Belfast (−CA), *Jenkins TM 6876;* Belfast (−CA), *Leendertz 2699;* Machadodorp (−CB), *Galpin 13104;* Skoonwater Farm (−CD), *Smook 894;* Nelshoogte (−DB), *Muller 2125;* Devils Kantoor, Kaapsehoop (−DB), *Pole Evans 1006.* 2531 (Komatipoort): Twello Forest (−CC), *Buitendag 699;* Schagen (−CC), *Liebenberg 2400;* Barberton (−CC), *Pott-Leendertz 5522;* Barberton (−CC), *Pott-Leendertz 5523;* Barberton Dist. (−CC), *Rogers 30270.* 2628 (Johannesburg): Turffontein (−AA), *Bryant* D3; Houghton Estate, (−AA), *Bryant* C49; Crescent Creek (−AA), *Cook 875;* Germiston (−AA), *Fenn PRE 316;* Johannesburg (−AA), *Leendertz TM 6058;* Kelland (−AA), *Liebenberg 8413;* Elsburg (−AA), *Rogers 12132;* Klipriviersberg (−AC), *Marloth 3858;* Suikerbosrand Nature Reserve (−CA), *Bredenkamp 853.* 2629 (Bethal): Ermelo Dist. (−DB), *Kuhne PRE 33937.* 2630 (Carolina): Carolina Dist. (−AA), *Burtt Davy 7367;* Leeuwpoort (−AA), *Burtt Davy 7446;* Chrissiemeer (−AC), *Theron 2408;* Coalbank Siding (−AD), *Malcolm PRE 7806;* Mavieriestad East (−CA), *Pott-Leendertz 5214* Athole Pasture Research Station (−CB), *Norval 57.*

O.F.S. — 2729 (Volksrust): Mont Pelaan (−DC), *Ferreira FO38.*

Swaziland.— 2631 (Mbabane): Mbabane (−AC), *Burtt Davy 2872;* Dalriach (−AC), *Compton 27158;* 16 km E of Mbabane (−AD), *Edwards 309.*

Natal. — (Vryheid): Wakkerstroom (−AD), *Smook 1202;* Vryheid Dist. (−CD), *Burtt Davy 11424.* 2731 (Louwsburg): Ngomi Forest (−CD), *Gerstner 4476;* Lower Mkuze Valley (−DA), *Ward 7269.* 2828 (Bethlehem): Royal Natal National Park (−DB), *Galpin 10353.* 2829 (Harrismith): Acton Homes (−CB), *Doidge 33939;* Mnweni, Drakensberg (−CC), *Esterhuysen 18675.* 2830 (Dundee): Oudeni, Ntschiza (−DB), *Edwards 2228;* Kranskop (−DD), *Stirton 5208.* 2831 (Nkandla): Umfulazane, Melmouth Dist. (−DB), *Mogg 4567.* 2832 (Mtubatuba): Hluhluwe Game Reserve (−AA), *Hitchins 106.* 2929 (Underberg): Cathkin Peak (−AB), *Gluckman 24963;* Giant's Castle (−AB), *Nicholson 2;* Giant's Castle (−AB), *Trauseld 845;* Tabamhlope Reserve (−BA), *West 458;* Drakensberg (−CB), *Werderman 1415.* 2930 (Pietermaritzburg): Shafton, Howick (−AC), *Hutton TM 2672;* Ligetton (−AC), *Mogg 1406;* Caversham (−AC), *Mogg 2402;* Tweedie (−AC), *Mogg 3467;* Balgowan, Glen Arum (−AC), *Mogg 5599;* Balgowan (−AC), *Stirton 5411;* Greytown (−BA), *Stirton 5086;* Zwartkop Location, Lions River (−CB), *Moll 1117;* Cedara Agricultural College (−CB), *Phillips 3452;* Drummond (−DA), *Galpin 10284;* Key Ridge, Drummond (−DC), *Stirton 5558;* Kloof, Pinetown Dist. (−DD), *Galpin 12260;* Claremont (−DD), *Medley-Wood 7648;* Gillits, Pinetown Dist. (−DD), *Moll 1922.* 3029 (Kokstad): Bushman's Nek (−AB), *Smook 1702.* 3030 (Port Shepstone): Mgaye (−BC), *Rudatis 733;* Mgayi (−BC), *Ward 6333;* Scottburgh (−BD), *Goossens 1703;* Murchison Flats (−CC), *Maclean 322;* Port Shepstone (−CD), *Henrici PRE 33943.* 3130 (Port Edward): Port Edward (−AA), *Ward 6667; Port Edward (−AB), Du Toit 912;* Port Edward (−AB), *Du Toit 942.*

Cape. — (Kokstad): Kokstad (−CB), *Coleman 924.* 3126 (Queenstown): Hangklip Mt. (−DD), *Galpin 5858.* 3127 (Lady Frere) Kopshorn (−BA), *Viljoen 193.* 3129 (Port St. Johns): Ntsubane (−BC), *Strey 9001.* 3227 (Stutterheim): Fort Cunynghame (−AD), *Sim 2792;* Ghulu Kop, Amatola Mts (−CA), *Dyer 255;* Nyameni Forest (−CA), *Dyer 256;* Gxulu Kop (−CA), *Gibbs Russell 3447;* Dohne Experiment Station (−CB), *Botha 9;* Evelyn Valley Forest (−CD), *Von Broembsen 116;* Kei Road Station (−DA), *Ranger 8.* 3228 (Butterworth): Kentani Dist. (−BC), *Pegler 70;* Kei Mouth (−CB), *Flanagan 928.* 3325 (Port Elizabeth): Atalaya Valley, Zuurberg (−BC), *Archibald 5283.* 3326 (Grahamstown): Grahamstown (−BC), *Britten 6492;* 8 miles from Grahamstown (−BC), *Comins 1014;* Grahamstown Dist. (−BC), *Godfrey SH1341;* On mountain, Grahamstown Dist. (−BC), *Zeyher 4466.*

C_3 Vouchers

Transvaal. — 2329 (Pietersburg): Top of Magoebaskloof Pass (−DD), *Ellis 3814.* 2430 (Pilgrim's Rest): Drakensberg Mts, NE of Penge (−AD), *Ellis 2812, 2813, 2830.* 2529 (Witbank): 5 km from Middelburg (−CD), *Ellis 2836;* 2 km from Middelburg (−CD), *Ellis 3811.* 2530 (Lydenburg): 5 km from Machadodorp (−CB), *Ellis 3812.* 2628 (Johannesburg): Delmas (−BA), *Ellis 3806.* 2629 (Bethal) 32 km from Middelburg (−BA), *Ellis 3809.* 2730 (Vryheid): Kwamandlangampisi Mts (−BA), *Ellis 3533.*

Natal. — 2729 (Volksrust): Majuba Pass (−BD), *Ellis 3768.* 2731 (Louwsburg): 16 km from Ngome Forest (−CD), *Ellis 3348.* 2929 (Underberg): Cathedral Peak Forest Reserve (−AD), *Ellis 3271;* 21 km from Estcourt (−BB), *Ellis 3773.* 2930 (Pietermaritzburg): 8 km from Balgowan (−AC), *Ellis 3774.* 3030 (Port Shepstone): 7 km from Highflats (−AC), *Ellis 3804;* Trafalgar Beach (−CD), *Ellis 3779;* Izotsha Station (−CD), *Ellis 3797.*

CONCLUSION

The variation within *Alloteropsis semialata* in leaf blade anatomy and photosynthetic pathway is recognized at the level of subspecies. This rank is chosen because, although the taxa are separate in southern Africa, their behaviour throughout their entire range is not known. Intermediate photosynthetic types occur in tropical Africa. Ellis (1981) reports that *Milne-Redhead* 3021 from Mwinilunga District, Zambia, has an intermediate carbon isotope ratio of −20,0 and is the only known example of a grass with this intermediate state. Three specimens from tropical Africa appear to be intermediate in the morphological characters that indicate the photosynthetic pathway as shown in Fig. 4. These are *Eyles* 1920 from Harare, Zimbabwe, *Greenway* 6290 from Chinjanje Valley, Malawi, and *Milne-Redhead* 3371 from Mwinilunga District, Zambia.

These intermediate forms merit closer study, especially because a species with anatomical characteristics intermediate between C_3 and C_4, *Neurachne lanigera* S.T Blake, has been reported from Australia (Hattersley *et al.*, 1982). This indicates that the situation in *Alloteropsis* may not be unique, and that within the Paniceae the understanding of the differences in photosynthetic pathways may lead to a clearer understanding of their evolution.

The taxonomic evaluation of anatomical and physiological data and its correlation with morphological characters presented in this paper has been possible only because voucher herbarium specimens prepared by Ellis and his co-workers were available. It is an outstanding example of the fact that taxonomy can fulfil its synthesizing role of evaluating as many characters as possible only when work done in other botanical disciplines is permanently recorded by voucher specimens. The voucher specimens establish the link between the morphological characters visible on the specimens, the distribution data recorded on the label, and the results of experimental or anatomical investigations.

ACKNOWLEDGEMENTS

R.P. Ellis, whose work originally discovered the problem, has assisted by providing the specimens and anatomical data which made this study possible, examining type specimens at Kew, and criticizing the manuscript. O.A. Leistner and L.E. Codd have given advice about taxonomic treatment. Mrs W. Roux has helped prepare the figures.

UITTREKSEL

Alloteropsis semialata *(R. Br.) Hitchc.* sensu *Chippindall (1955) en Clayton (in druk) is die enigste bekende grasspesie met beide Kranz en nie-Kranz blaaranatomie en dus met beide die C_3 en C_4 fotosinteseroetes. In die verlede is twee taksons erken maar die kenmerke wat gebruik is om hulle te skei, is as onbetroubaar bewys. Gevolglik is hulle verenig. Die sorgvuldige bestudering van kontrole herbariumeksemplare vir anatomiese en fisiologiese werk het egter getoon dat C_3 en C_4 taksons geskei kan word op grond van morfologiese kenmerke wat verskil van dié wat in die verlede gebruik is. Twee taksons word gevolglik weer erken op die subspesievlak en die naam* Alloteropsis semialata *subsp.* **eckloniana** *(Nees) Gibbs Russell* stat. nov. *word gepubliseer.*

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Bothalia 14, 2: 215–217 (1983)

A karyotypic and anatomical study of an unidentified liliaceous plant

J. J. SPIES* and D. S. HARDY*

ABSTRACT

An unidentified sterile liliaceous plant and three possible relatives were studied karyotypically and anatomically. All these plants have a somatic chromosome number of 2n = 14. The possibility of the sterile plant having arisen as a result of a mutation appears unlikely, when compared with the possibility of hybrid origin. Chromosome morphology rules out *Bulbine latifolia* (L.f.) R. & S. and *Aloe arborescens* Mill. as possible parents. The sterile plant and *Aloe marlothii* Berger have similar karyotypes and, therefore, *A. marlothii* may be one of the parents. A close relationship between the sterile plant and the genus *Aloe* is further confirmed by their similar epidermal structure.

INTRODUCTION

A curious, liliaceous plant, apparently unknown to science, was found in a neglected garden in Pretoria during 1970. The plant has distichous leaves and a short almost prostrate stem and obviously belongs to the Liliaceae, but flowering material was required for a positive identification. The plant was transplanted to the Pretoria National Botanical Garden but, for the past 12 years, all attempts to induce flowering have proved unsuccessful and it therefore appears to be sterile.

The sterility of the plant may be due to genetic factors, or may indicate a hybrid origin. A search for possible parents revealed only three likely plants in close proximity to the sterile plant, namely *Aloe arborescens* Mill. *A. marlothii* Berger and *Bulbine latifolia* (L.f.) R. & S. This investigation attempted, by karyotypic and anatomical methods, to establish whether hybridization between any of these species could have resulted in this unidentified plant.

MATERIALS AND METHODS

Root tip material of *Aloe arborescens* (*Hardy* 6045), *A. marlothii* (*Henderson* 352), *Bulbine latifolia* (*Mauve* 4995) and the supposed hybrid (*Hardy* 6055) were collected in the Pretoria National Botanical Garden and pretreated in monobromonaphthalene at room temperature. After four hours, the root tips were washed in running water and fixed in Carnoy fixative (Darlington & La Cour, 1976) for 24–36 hours. After hydrolysis for 10 minutes at 60° C in 1N HCl, the material was stained in leucobasic fuchsin (modified formula after Coleman, 1938; Darlington & La Cour, 1976) for 2 hours. The darkly stained parts were then squashed in aceto-orcein (La Cour, 1941). Slides were made permanent by placing them in a fridge for ±10 minutes, removing the coverslip with a needle, dehydrating through an alcohol series and mounting in Euparal. Ten cells per plant were studied.

Leaf segments were boiled for 10 minutes in concentrated HNO_3 to prepare epidermal peels. The epidermis was separated from the rest of the leaf during this process and was removed from the debris, stained in Methylene Blue, dehydrated in alcohol and mounted in Euparal.

Voucher specimens of the material studied are lodged in the National Herbarium, Pretoria.

RESULTS

(a) Bulbine latifolia

A somatic chromosome number of 2n = 14 for this species, as reported by Snoad (Darlington & Wylie, 1955) and Jones & Smith (1967), was confirmed. The haploid karyotype (Fig. 1) consists of two large metacentric to submetacentric, two large subtelocentric and three small subtelocentric chromosomes. An idiogram (Fig. 1a) has been compiled from the data given by Jones & Smith (1967). The results of the present study are shown in Fig. 1b.

The two idiograms illustrate small differences in the karyotypes. The present study revealed the second chromosome pair to be submetacentric, whereas the published data show a metacentric chromosome pair. The fourth chromosome pair was found to be of similar length to the third pair, but with the centromeric index slightly lower. Although Jones & Smith also found the fourth pair to be more subtelocentric than the third, the two pairs could also be distinguished by a marked variation in length. The third difference observed in this study lies in the presence of satellites on the long arms of the fifth chromosome pair. No satellites were reported by Jones & Smith (1967).

These karyotype differences between the published and observed data indicate the existence of chromosomal variability in *B. latifolia.* A cytotaxonomic study of this species should prove valuable.

(b) Aloe arborescens

A somatic chromosome number of 2n = 14 was observed and confirms reports in the literature (Taylor, 1925; Ferguson, 1927; Resende, 1937; Muller, 1941; Snoad, 1951; Sharma & Mallick, 1966). The haploid idiogram (Fig. 2) illustrates four long subtelocentric chromosomes and three short subtelocentric ones. Satellites are present on the distal part of the long arms of the fourth chromosome pair. Apart from the SAT-region on the fourth chromosome pair, no secondary constrictions, as described by Sharma & Mallick (1966), were observed.

(c) Aloe marlothii

A somatic chromosome number of 2n = 14 was found and agrees with reported observations (Resende, 1937; Riley, 1959). The haploid idiogram (Fig. 3) shows four long and three short subtelocen-

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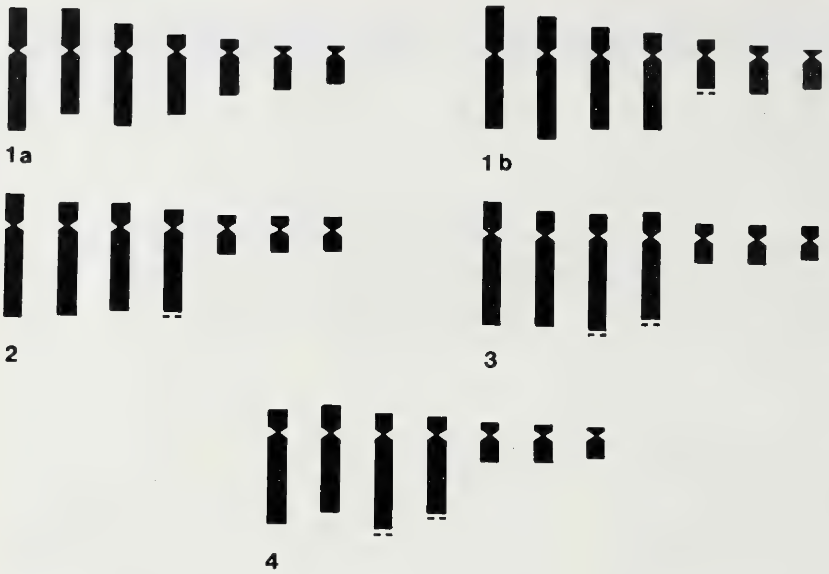


FIGS 1–4.—Haploid idiogram. 1, *Bulbine latifolia:* a, compiled from Jones & Smith, 1967; b, this study. 2, *Aloe arborescens.* 3, *A. marlothii.* 4, sterile plant.

tric chromosomes. Satellites were seen on the distal part of the long arms of the third and fourth chromosome pairs. The karyotypes of *A. marlothii* and *A. arborescens* correspond in all respects, except for the satellites on the third chromosome pair.

(d) The unknown liliaceous plant

This plant has 14 chromosomes per somatic cell. All chromosomes are subtelocentric with eight long and six short chromosomes (Fig. 4). The third and fourth chromosome pairs have satellites on the distal parts of the long arms. These satellite-bearing chromosomes have slightly larger arm ratios than the other long chromosomes (Fig. 4). The karyotype suggests that the chromosomes might be arranged in seven homoeologous pairs with no, or very small differences being visible between the chromosomes within a pair.

Morphology and epidermal structure. The small distichous-leaved plant produces suckers. The mother plant is c. 60 mm tall with c. 9 pairs of smooth, linear-acuminate, succulent, unequal leaves, the longest c. 60 mm long and c. 10 mm broad with a few small teeth at the apex. The morphology of the different plants can be seen in Figs 5–8.

The epidermis of *Bulbine latifolia* consists of elongated quadrangular cells (Fig. 9). Both the *Aloe* species, and the sterile plant, have hexagonal epidermal cells. Epidermal cells of *A. arborescens* (Fig. 10) are smaller than the cells of *A. marlothii* (Fig. 11) and the sterile plant (Fig. 12).

DISCUSSIONS AND CONCLUSIONS

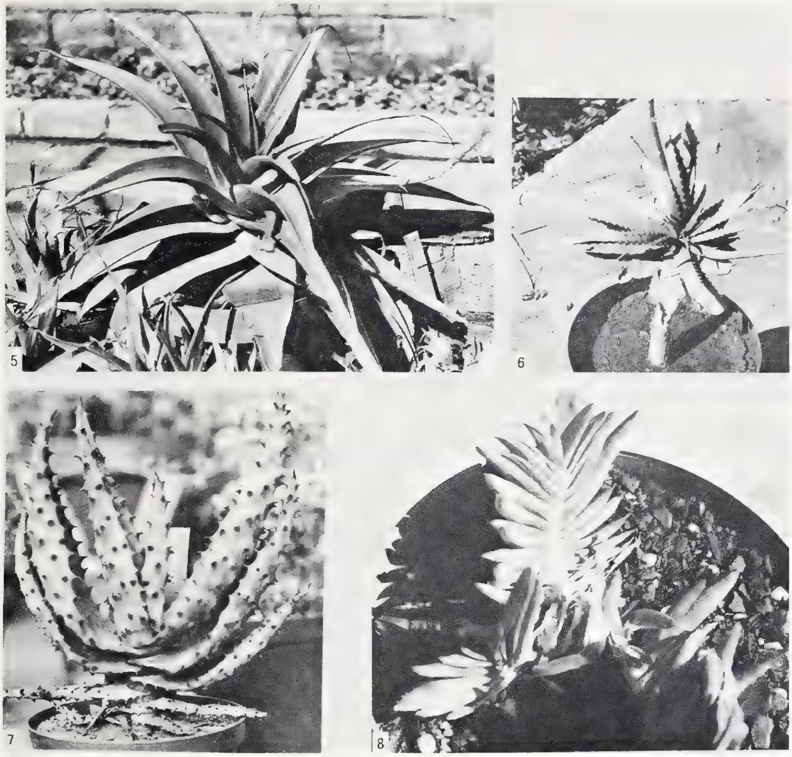
The sterile plant might represent an undescribed species or may have originated by hybridization or by mutation. If it is a hybrid, the parents must have occurred in the vicinity of the hybrid and the hybrid will have one genome from each parent. Since all possible parental species in close proximity to the sterile plant have been investigated, the similarity between genomes might have an indication of relationships.

A comparison of the haploid idiogram of the possible hybrid with that of *Bulbine latifolia* reveals large differences. The presumed hybrid has no chromosomes that are nearly metacentric as in *B. latifolia* and the short-satellited chromosomes of *B. latifolia* are absent in the hybrid. If *B. latifolia* was one of the parental species, the resulting hybrid must have received at least two large metacentric chromosomes and a short chromosome with satellites from this source. This observation indicates that *B. latifolia* could not have been one of the parents. Further evidence for this is illustrated by the epidermal structure, where *B. latifolia* has a totally different epidermal structure from the hybrid which has a typical *Aloe* pattern (Figs 9–12).

The epidermal structure of the hybrid corresponds closely with the patterns found in *Aloe arborescens* and *A. marlothii* (Figs 10–12). A closer relationship between the hybrid and the Aloes studied is further confirmed by the similarity in their karyotypes. However, as the hybrid has two satellited chromosome pairs and *A. arborescens* only one, *A. arborescens* is an unlikely parent. The karyotypes of *A. marlothii* and the hybrid agree in almost all respects. The only observed differences were in the arm ratios of the first two chromosome pairs. These small differences might result from a statistically inadequate sample, or from the fact that the first two pairs are of almost similar length and the first and second pair might be interchanged in the presumed hybrid.

If the sterile plant is the product of mutation, the parents must have a karyotype similar to *A. marlothii.* The chances of a mutation transforming a fertile plant, a few metres tall, to a 6 cm sterile plant and hard thorny leaves to smooth fleshy leaves at the same time seems very unlikely. The suggestion of hybridization seems more probable.

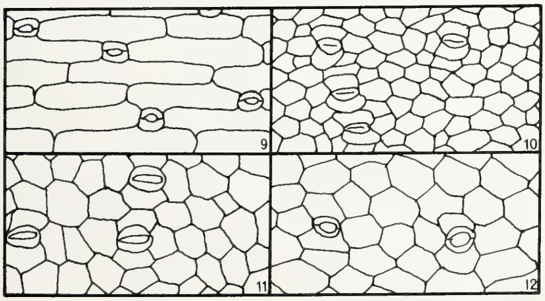
The restricted growth habit and absence of flowers in the sterile plant suggest hybridization rather than a new species. The similarity between the sterile plant and *A. marlothii* with regard to



FIGS 5–8.—Photographs of studied plants. 5, *Bulbine latifolia;* 6, *Aloe arborescens;* 7, *A. marlothii;* 8, sterile plant.

karyotype and epidermal structure make it reasonable to suggest that *A. marlothii* might be one of the parents. Although no other possible parent was found in the vicinity of the supposed hybrid plant, a hybrid origin for the sterile plant is still possible. The second parent might have died by the time the hybrid was discovered. It is also possible that the hybrid was introduced into the area where it was found.

The results of this study indicate, therefore, that the sterile plant is a hybrid between *A. marlothii* and another species of *Aloe*.



FIGS 9–12.—Drawings of epidermal patterns. 9, *Bulbine latifolia;* 10, *Aloe arborescens;* 11, *A. marlothii;* 12, sterile plant.

UITTREKSEL

'n Ongeïdentifiseerde steriele plant van die familie Liliaceae en drie moontlik verwante plante is kariotipies en anatomies bestudeer. Al hierdie plante het 'n somatiese chromosoomgetal van 2n = 14 gehad. Die waarskynlikheid dat die steriele plant 'n baster is, is groter as die moontlikheid van 'n mutasie oorsprong. Op grond van chromosoommorfologie word Bulbine latifolia *(L.f.) R & S. en* Aloe arborescens *Mill. as moontlike ouers uitgeskakel. Die steriele plant en* A. marlothii *Berger het ooreenstemmende kariotipes en daarom kan* A. marlothii *een van die ouers wees. Die verwantskap tussen die steriele plant en die genus* Aloe *word verder bevestig deur ooreenstemmende epidermale strukture.*

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Bothalia 14, 2: 219–222 (1983)

Notes on African plants

VARIOUS AUTHORS

APOCYNACEAE

THE CORRECT AUTHOR CITATION FOR *PACHYPODIUM SUCCULENTUM*

Pachypodium succulentum (*L.f.*) *Sweet,* Hort. Brit. ed. 2: 594 (1830); A.DC. in DC., Prodr. 8: 424 (1844); Stapf in Fl. Cap. 4,1: 517 (1907), as *P. succulentum* (Thunb.) A.DC.; Codd in Fl. S. Afr. 26: 285 (1963), as *P. succulentum* (L.f.) A.DC.; Mabberley in Taxon 29: 605 (1980), as *P. succulentum* (Jacq.) Sweet.

Echites succulenta L.f., Suppl. 167 (1781); Thunb., Prodr. 37 (1794); Jacq., Fragm. bot. 74, t. 117 (1809); Thunb., Fl. Cap. ed. Schult. 232 (1823).

For some years the author citation for *Pachypodium succulentum* was referred to as (L.f.) A.DC. Mabberley, *l.c.,* reported an earlier combination by Sweet and listed the authority as (Jacq.) Sweet. Sweet cited the basionym as *Echites succulenta* Jacq. but Jacquin did not claim to be the author. He referred to the species as *Echites succulenta* Thunb. and Thunberg (1823) included 'Linn. Suppl. p. 167' among his references, thus leading one to the original description.

L.E. CODD

CELASTRACEAE

A NEW NAME FOR *HARTOGIA* THUNB. EX L.f.

Hartogiella *Codd,* nom. nov.

Hartogia Thunb. ex L.f., Suppl. 16 (1782), non L. (1759). Type species: *H. capensis* L.f., Suppl. 128 (1782), non L. (1759).

Schrebera Thunb., Prodr. 28 (1794), non L. (1763). Type species: same as for *Hartogia* Thunb. ex L.f.

Hartogiella schinoides (*Spreng.*) *Codd,* comb. nov.

Elaeodendron schinoides Spreng., Syst. 1: 780 (1824). *Schrebera schinoides* Thunb., Prodr. 28 (1794), non L. (1763). *Hartogia schinoides* C. A. Sm. in Jl S. Afr. For. Ass. 20: 50 (1951). Type: as for *H. capensis* L.f.

Hartogia capensis L.f., Suppl. 128 (1782), non L. (1759). Type: Grootvadersbosch and Riviersonderend, *Thunberg.*

H. multiflora Eckl. & Zeyh., Enum. pl. afr. austr. 127 (1834/35). *H. capensis* var. *multiflora* (Eckl. & Zeyh.) Sond. in Fl. Cap. 1: 464 (1860). Type: Cape, 'Tulbaghsberge', *Ecklon & Zeyher* (PRE, iso.).

H. riparia Eckl. & Zeyh., l.c. 127 (1834/35). *H. capensis* var. *riparia* (Eckl. & Zeyh.) Sond., l.c. 464 (1860). Type: Cape, Berg River near Saldanha Bay, *Ecklon & Zeyher.*

H. capensis var. *lanceolata* Sond., l.c. 464 (1860). Type: as for *H. capensis* L.f.

H. angustifolia Turcz. in Bull. Soc. Nat. Moscow 36: 601 (1863). Type: Cape, *Zeyher* 307.

C. A. Smith, *l.c.,* pointed out that *Hartogia capensis* L.f. and *Schrebera schinoides* Thunb. are later homonyms of *H. capensis* L. (1759) (Rutaceae) and *S. schinoides* L. (1763) (Convolvulaceae), respectively, and are, therefore, illegitimate. He also stated that, at the International Botanical Congress held in Cambridge in 1931, the generic name *Schrebera* Roxb. was conserved against *Schrebera* L. (and hence against *Schrebera* Thunb.) and *Hartogia* Thunb. ex L.f. against *Hartogia* L.

Although it is on record that *Schrebera* Roxb. has been conserved, no evidence can be found that *Hartogia* Thunb. ex L.f. received similar recognition. The latter is a small genus of one or two species (one in South Africa and one of doubtful status, *H. agrifolium* Chiov., described from Somalia), with little or no ecological or economic significance. It is, therefore, unlikely that a case for conservation of the generic name would now be considered favourably.

In establishing the correct species name for the South African plant, it was found that K. Sprengel, Syst. 1: 780 (1824), had taken up the Thunberg epithet as *Elaeodendron schinoides.* Because Thunberg's epithet is illegitimate, Sprengel did not effect a combination but a new name dating from 1824, and this appears to be the earliest legitimate name for the plant. A few years later Ecklon & Zeyher published two further names based on their own specimens. All these were overlooked by Smith when he adopted the illegitimate Thunberg epithet 'schinoides' as a new name, *Hartogia schinoides* C. A. Sm. (1951).

L.E. CODD

LAMIACEAE

A NEW SUBSPECIES IN *OCIMUM*

Ocimum urticifolium *Roth* subsp. **caryophyllatum** *Codd,* subsp. nov., a typo caulibus elatioribus lignosioribus, foliis parvioribus subintegris, inflorescentiis brevioribus differt.

TYPE.—Natal, 2832 (Mtubatuba): Mapelana Forest, south of St Lucia Estuary (–AD), *Cooper 119* (PRE, holo.).

Perennial soft shrub 1–2 m tall, branching mainly in the upper part; stems woody below, herbaceous above. *Leaves* petiolate; blade ovate-elliptic to elliptic, 30–50 × 18–20 mm, freely gland-dotted, puberulous on the nerves on the upper surface, otherwise glabrous, apex acute, base cuneate, margin shallowly crenate-dentate to subentire; petiole 10–30 mm long. *Inflorescence* terminal, spikelike, solitary or several together due to the stems branching near the apex, 35–60 mm long;

verticils usually 6-flowered, about 5 mm apart; bracts broadly ovate, acuminate, 4–6 mm long; pedicels 3 mm long. *Calyx* 5–6 mm long at maturity; upper tooth broadly ovate, decurrent; lateral teeth small, subulate; lower lip oblong, shortly 2-toothed, eventually bending upwards closing the mouth of the calyx. *Corolla* white, 4 mm long, bilabiate. *Stamens* exserted by 3 mm.

Recorded from the margins of dune forest along the coast of northern Natal.

NATAL.—2831 (Nkandla): Twin Streams, Mtunzini (–DD), *Strey 6450; Jenkins* s.n. 2832 (Mtubatuba): Mapelana Forest, south of St Lucia Estuary (–AD), *Cooper 119; Palm Ridge farm, Harrison 210.*

O. urticifolium is a widespread and variable species extending from Asia to tropical Africa and into southern Africa as far south as Durban. In southern Africa the typical form is a soft, branched shrub up to about 1 m tall with large dentate leaves 45–120 × 25–60 mm, and the inflorescences are normally 100–200 mm long. Subsp. *caryophyllatum* is a more woody shrub growing 1–2 m tall which branches mainly in the upper half of the plant; the leaves tend to be smaller, with inconspicuously toothed margins, and the inflorescences are consistently shorter. In floral characters, subsp. *caryophyllatum* cannot be distinguished from the typical plants, so infraspecific status is considered to be appropriate for it. Apparently living plants of the two forms may be distinguished by the scent of the leaves. Typical plants, at least in Natal, have leaves which are lemon-scented, whereas the leaves of subsp. *caryophyllatum* are reported to smell of cloves or nutmeg.

L.E. CODD

LILIACEAE

AN INTERESTING PLANT RECORD FROM THE GULF OF ADEN AREA

During a brief visit to the Yemen in March–April 1974, the author spent some time making botanical collections along the WSW slopes and on the summit plateau of the Jabal Sumara, north of the town of Ibb.

Despite the unfavourable season at the very beginning of the spring rains, considerable material, both live and dried was brought together.

A special search was made for *Kniphofia sumarae* Defl., which had not been collected since Deflers's noteworthy journey to the High Yemen in 1887. Numerous plants, recognizable by their dried leaves, were found at an altitude of between 2 900 and 3 050 m in a narrow valley leading off to the south at the highest point of the new motor road over the mountains from Ibb to Yarim.

In its natural habitat, *K. sumarae* grows on moist, rocky slopes, heavily overgrazed and eroded. Its associates are *Aloe tomentosa* Defl., *Centaurea maxima* Forsk., *Trifolium semipilosum* Fresen., *Daucus yemensis* Defl., *Macowania ericifolia* (Forsk.) Burtt & Grau, *Alkanna* sp. cf. *A. orientalis* (L.) Boiss., *Erica arborea* L. and others. It seems that these highlands were wooded with *Juniperus* Forest before the heavy hand of man reduced them to their present depauperated state.

Flowering material obtained in cultivation from some of the plants collected at this locality (*Lavranos* 11292, 26 March 1974), makes it possible to give a more detailed description of this interesting species which, in certain respects, complements the original one by Deflers.

Our flowering material of *K. sumarae* (Fig. 1) agrees fairly well with Deflers's description of the species and with that of Marais in Kew Bull. 28,3: 482–483 (1973). However, the perianth tube, narrowly campanulate in its lower part, widens abruptly from about the middle; the filaments shorten only slightly after anthesis; the style, in fresh material, is never exserted beyond 2,5 mm; the flowers are pale yellow and rather strongly scented.

It is worthy of note that this species has no obvious close relatives within the general area where it grows. It seems to be related, at least where the perianth form is concerned, to certain species from Southern Africa, notably *K. acraea* Codd and *K. brachystachya* (Zahlbr.) Codd. With these, and with the related *K. typhoides* Codd and *K. umbrina* Codd and some others, it also has in common scented flowers. The geographical isolation of *K. sumarae* from the above species makes it difficult to postulate

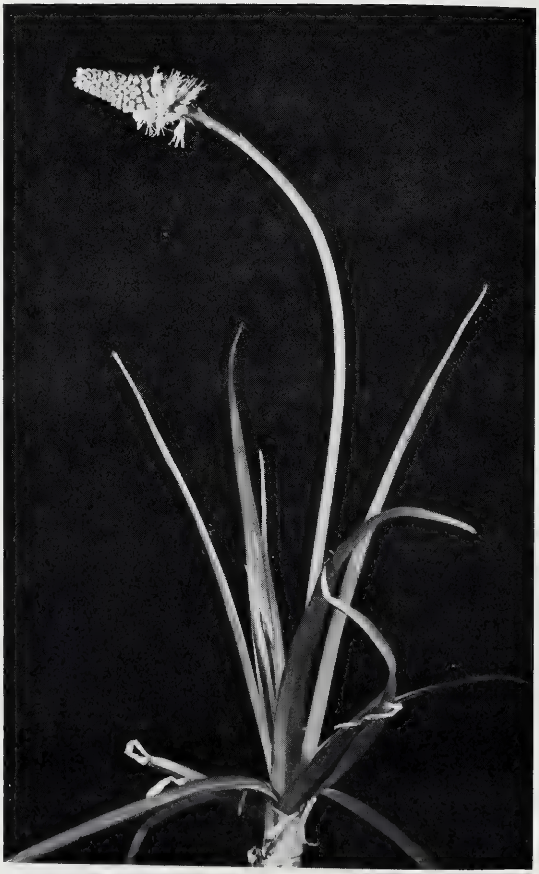

FIG. 1.—*Kniphofia sumarae* flowering in cultivation (*Lavranos* 11292).

their derivation from a common ancestor within the genus. One may rather assume that the genus contains (or did in the past) one or more genetic factors prone to mutate at different times and places but in the same manner, giving similar character combinations. Marais *l.c.* rightly states that *K. sumarae* forms a good link between the species formerly placed in *Notosceptrum* Benth. and such taxa as *K. pumila* (Ait.) Kunth and *K. foliosa* Hochst.

In addition to the type gathering and the present collection at the same locality, *K. sumarae* was collected by Botta in 1837 near the summit of Jabal Sabir (3 008 m) south of Ta'izz.

DESCRIPTION.—Plants rhizomatous, their leaves dying off during the dry (winter) season, their rootstock rather robust and fleshy, mostly simple, occasionally 1- or 2-branched. *Leaves* ensiform, carinate, acute, erect, 30–50 cm long, c. 15 mm broad at base, bright green, rather soft and fleshy; margins serrulate-ciliate, keel smooth except in the apical portion where it is serrulate; remains of dry leaves fibrous, rather tough. *Inflorescence* simple, 50–100 cm tall; peduncle 5–7 mm diam., terete, glabrous, green with 6–8 deltoid, acute, 1-nerved sterile bracts the lowest of which are usually green, fleshy, ensiform with acute apex and ciliate margins, c. 20 mm long and 5 mm wide, while the upper are scarious, brownish, up to 7 mm long, decreasing upward in size. *Raceme* densely flowered, conical, 80–100 mm long, elongating to 15–200 mm when in fruit, flowers held horizontally. *Bracts* ovate-lanceolate deltoid, brown, scarious, 3,5–5,0 mm long with acute or rounded apex. *Flowers* pale yellow, with one indistinct green nerve from base of tube to apex of segments. *Pedicels* 1 mm long elongating to about 3 mm when in fruit. *Perianth* funnel-shaped, 8–9 mm long, cylindric in its lower half, flaring abruptly from about the middle, 2 mm wide over the ovary, 4 mm at mouth; tube 5,5–6,0 mm long, segments oblong, free for 2,5–3,0 mm their apex straight (not reflexed). *Filaments* pale yellow, terete, tapering towards the apex, the anthers broad, two-lobed, in turn exserted by 5 mm. *Style* terete, the stigma at length exserted by about 2 mm. *Ovary* green, 2 mm long, 1,2 mm diam., narrowly ovoid in long section, obtuse at apex.

J.J. LAVRANOS

TILIACEAE

A NEW SPECIES OF *CORCHORUS*

Corchorus psammophilus *Codd*, sp. nov., *C. asplenifolio* Burch. et *C. confuso* Wild affinis, sed foliis ovato-oblongis, margine minute crenulato differt.

Herba perennis, radice lignosa; caules prostrati, tenues, simplices vel parce ramosi, 300–600 mm longi, villosi. *Folia* petiolata; lamina ovato-oblonga vel late elliptica, griseo-viridis, strigosa, 30–45 × 15–20 mm, nervis subtus valde prominentibus, apice rotundato, basi rotundata vel truncata, margine minute crenulato; petiolus 3–6 mm longus, hispidus; stipulae setaceae, 5–6 mm longae, pilosae. *Cymae* suboppositifoliae, subsessiles vel breviter pedunculatae, 1–3-florae; pedicelli 6–8 mm longi, recurvi; bracteae setaceae, 4–5 mm longae. *Sepala* anguste lanceolata, acuminata, 7–9 × 1,5 mm, extus villosa. *Petala* flava, oblanceolata vel obovata, 6–8 × 3– 5 mm, breviter unguiculata. *Androgynophorum* 0,5 mm altum. *Stamina* numerosa, filamentis ca 4 mm longis, antheris 0,5 mm longis. *Ovarium* 3-loculare, anguste ellipticum, dense strigosum; stylus 7 mm longus, glaber; stigma fimbrillatum. *Capsula* trivalvis, cylindrica, subarcuata, strigosa, 18–25 × 2 mm, multisperma. *Semina* oblonga, 1,75 × 1 mm, nigrescentia.

TYPE.—Transvaal, 2327 (Ellisras): 5 km N. of P. O. Ons Hoop (–DA), *Codd 8460* (PRE, holo.)

Perennial herb with several prostrate, slender, simple or sparingly branched, villous stems 300–600 mm long, radiating from a slender woody tap-root. *Leaves* petiolate; blade ovate-oblong to broadly elliptic, grey-green, 30–45 × 15–20 mm, strigose on both surfaces, nerves prominent below, apex rounded, base rounded to truncate, margin minutely crenulate; petiole 3–6 mm long, hispid; stipules setaceous, 5–6 mm long, pilose. *Cymes* subopposed

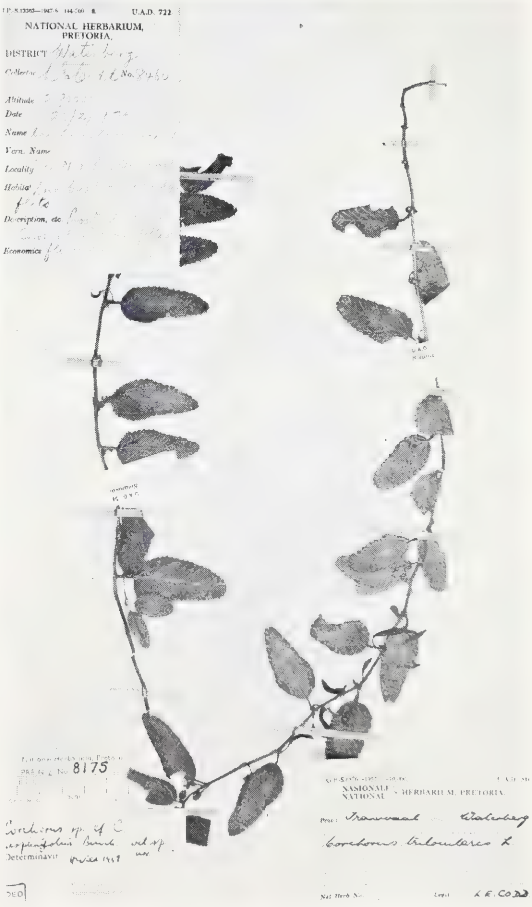

FIG. 2.—Holotype of *Corchorus psammophilus*, *Codd* 8460.

to the leaves, subsessile to shortly pedunculate, 1–3-flowered; pedicels 6–8 mm long, recurved; bracts setaceous, 4–5 mm long. *Sepals* narrowly lanceolate, acuminate, 7–9 × 1,5 mm, villous without. *Petals* yellow, oblanceolate–obovate, 6–8 × 3–5 mm, shortly clawed. *Androgynophore* 0,5 mm long. *Stamens* numerous, filaments about 4 mm long, anthers 0,5 mm long. *Ovary* 3-locular, narrowly ellipsoid, densely strigose; style 7 mm long, glabrous; stigma fimbrillate. *Capsule* 3-valved, cylindrical, somewhat arcuate, strigose, 18–25 × 2 mm, many-seeded. *Seeds* oblong, 1,75 × 1 mm, blackish (Fig. 2).

This species is related to *C. asplenifolius* Burch. and *C. confusus* Wild, but differs from both in the ovate-oblong to broadly elliptic leaves with finely crenulate margins and very prominent nerves on the undersides. It was first collected in February 1954 on the farm Zonderwater No. 1377, 5 km N. of Ons Hoop, in the Ellisras area and again recently, somewhat further west, associated with sandy *Terminalia* veld.

TRANSVAAL.—2327 (Ellisras): Van der Waltspan, between Ellisras and Stockpoort (–CB), *Smook 4320a.*

The following key to the Southern African species of *Corchorus* is based on a revision of the genus (unpublished) undertaken for the Flora of Southern Africa by Prof. H. Wild some years ago.

1. Leaves variously pubescent or glabrous but not tomentose:
  2. Capsule 10-ribbed, 5-valved .... 1. *C. olitorius*
  2. Capsule 3–4-valved:
    3. Capsule with 3 spreading horns at the apex .... 3. *C. tridens*
    3. Capsule rostrate or blunt at the apex, without diverging horns:
      4. Leaves pinnatipartite, lobed 4/5 of the way to the midrib .... 9. *C. pinnatipartitus*
      4. Leaves serrate or crenate but not lobed:
        5. Annual herbs:
          6. Peduncles obsolete or up to 2 mm long, not filiform; leaves not linear:
            7. Capsules up to 70 mm long, held erect; valves minutely scabrous .... 2. *C. trilocularis*
            7. Capsules up to 25 mm long, usually curved, not held erect, angles muricate or sharply toothed .... 7. *C. schimperi*
          6. Peduncles filiform, up to 20 mm long; leaves linear .... 10. *C. longipedunculatus*
        5. Perennial herbs with annual, often prostrate stems from a woody rootstock, or a bushy perennial about 600 mm tall:
          8. Fruiting pedicel straight or more or less straight:
            9. Fruit valves hispidulous, rarely glabrescent; lateral nerves of leaves (excluding basal nerves) in 7– about 20 pairs; perennial herb with annual or little-branched stems from a woody rootstock .... 4. *C. confusus*
            9. Fruit valves glabrous or sparsely stellate-puberulous when young; lateral nerves of leaves (excluding basal nerves) in 5 (–7) pairs; much-branched shrublet about 600 mm tall .... 11. *C. angolensis*
          8. Fruiting pedicel curved:
            10. Leaves glabrous or hispid to strigose, often with bulbous-based hairs:
              11. Leaves usually linear to narrowly oblong-lanceolate, if ovate then margin coarsely crenate-dentate .... 5. *C. asplenifolius*
              11. Leaves ovate-oblong to broadly elliptic, strigose, margin finely crenulate .. 6. *C. psammophilus*
            10. Leaves densely sericeo-villous on the lower surface, ovate to narrowly ovate-oblong, margin coarsely crenate-dentate .... 8. *C. sulcatus*
1. Leaves yellowish or greyish tomentose, at least below:
  12. Capsule cylindric or, if narrowly ellipsoid, with softish plumose bristles less than 2 mm long:
    13. Leaves ovate, grey-green; nerves in about 4 pairs .... 12. *C. merxmuelleri*
    13. Leaves narrowly oblong or narrowly elliptic to oblong or oblong-lanceolate, drying yellowish or brownish; nerves in 6–15 pairs:
      14. Indumentum very shortly and smoothly velvety; nerves rather inconspicuous, in 13–15 pairs; bracts up to 2 mm long .... 13. *C. velutinus*
      14. Indumentum often rather tufted and coarse or thick and felted; nerves conspicuously raised below, in 6–10 pairs; bracts up to 8 mm long .... 14. *C. kirkii*
  12. Capsule broadly ovoid and glabrous or ellipsoid with stiff plumose bristles about 5 mm long .... 15. *C. junodii*

L.E. CODD

Bothalia 14, 2: 223–236 (1983)

Centenary of the Natal Herbarium, Durban, 1882–1982

B. D. SCHRIRE*

ABSTRACT

The history of the Natal Herbarium is described from its inception in 1882 to 1982, the year of its centenary. Its history is inextricably linked with that of the Durban Botanic Gardens which started as an Agricultural Garden in 1848, and the Durban Botanic Station. The roles played by various curators and officers-in-charge, especially John Medley Wood, who held office for 32 years and did much to put the Herbarium on the botanical map, are emphasized.

AN AGRICULTURAL GARDEN NEAR DURBAN

Although Natal Herbarium began its existence officially in 1882, its colourful history goes back to 1848 when the then British colony of Natal was constituted a separate government. At this time the Natal Agricultural and Horticultural Society was formed in order to experiment with various economic plants for cultivation. The following advertisement heralded the occasion: 'A meeting will be held at the Commercial Hotel on Tuesday 18th April next, at 10 o'clock for the purpose of attempting to organise an Agricultural Society'. At this meeting, held in a small thatched building where the Royal Hotel stands today, office bearers and a committee were elected.

A second meeting in June led to an application being made to the Lieutenant Governor for a grant of a hundred acres at Umlaas, but this was refused. At a later meeting Dr Stanger, vice-president, and other committee members rode out to the Berea to select a suitable site and they finally decided on some land on the banks of the Umgeni River. Permission was then granted by the Governor to occupy this land pending approval by the Secretary of State. Mr Chas Johnson was appointed as the first overseer of the area on the 15th July 1849 and, instead of a salary, he was to sell the surplus products of the garden to cover his expenses.

The first agricultural show was held in 1850 in the Government school-room in the centre of the township and fruit, cotton, wheat, oats, yams and other vegetables were on display, although no flowers were shown. In spite of valuable prizes being offered to the public, the show was a failure and the newly formed society began to suffer through lack of practical support. Johnson left on 14th October 1850.

At a subsequent dinner at McDonald's Hotel, the society was virtually reorganized and a new board of officers and committee elected. The president was Mr Edmund Morewood of Compensation Estate to whom is attributed the first cultivation of sugar as a marketable product in Natal. The land near the Umgeni proved to be unsuitable because of inadequate soil and lack of available water so the Society selected and obtained a grant from the government for 25 acres of land at the foot of the Berea ridge near the site occupied by the kraals and gardens of Chief John Cane's following. The area was ideal because of the everflowing artesian wells represented even today by Curries Fountain from which Durban's water supply was drawn in the early years. The grant was later increased to 50 acres, although the title deeds were not received until 1854.

MARK JOHNSTON McKEN — FIRST CURATOR

Mark J. McKen, who had some experience of sugar-growing in Jamaica, had arrived in Natal from England in October 1850 and soon afterwards he joined the Society and injected new enthusiasm into it. The ultimate success of its fresh effort was largely due to the services of McKen who advocated the establishment of a Botanical Garden for the purpose of testing out and acclimatizing East Indian and South American plants. Among the various new

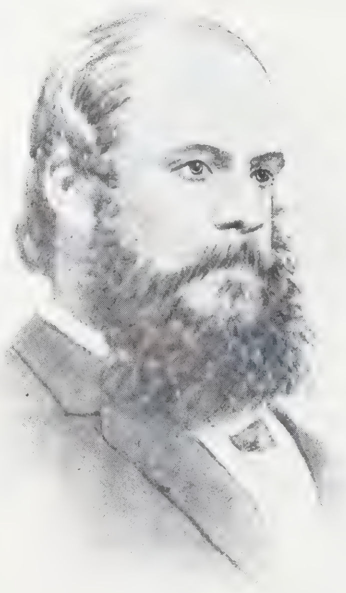

FIG. 1.—Mark Johnston McKen (1823–1872).

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introductions he brought with him from Kew were mangoes, breadfruit, ginger, coffee, arrowroot, camphor, pawpaw, guava, cocoa, cinnamon, blood orange, Assam Tea and black pepper, and these were first planted in Beningfield's property near the bay.

McKen (Fig. 1) was officially engaged as curator on 11th June 1851 at the 'staggering' salary of £50 per annum and a free hut to live in. During the first years all efforts were concentrated upon the introduction, propagation and distribution of plants considered to be suitable for commercial planting and at this stage arrowroot, coffee, tea and sugar gave the most success although, of these, only sugar remains an important product today. Arrowroot failed through lack of demand, the coffee plantations in Natal succumbed to a fungus disease and locally produced tea could not compete with the imported article.

The Society held its first show in its own grounds on 1st August 1851 and it was a gala day for everybody in town. Miss Forbes, in her account of the history of the Botanical Gardens, writes: 'All stores were closed during the morning and the majority of the townspeople found their way by the Pietermaritzburg road, and over the flat to the entrance of the Gardens.' Miss Forbes continues her account: 'Here a few poles and ships flags gave animation to the scene, while the exhibits were displayed on rough tables of yellow-wood planks, under an awning of wagonsails and evergreens. Farmers and visitors with their wagons and families all round, while children's voices and the curling smoke from under domestic kettles indicated a series of picnics within the shelter of the gardens. A lively interest was taken in this first most important occasion by the inhabitants generally, who had generously subscribed towards the prizes. This show was a success, happy and memorable; an occasion to be recollected by the new settler and his wife, who recognized the reproduction of the garden stuff which they believed grew nowhere outside England.'

In addition to the many kinds of fruit and vegetables displayed, tobacco, wheat, rice, coffee and pistachio nuts were offered. Great excitement prevailed over the ploughing match, which took place on the flat grassland at the lower part of the gardens, because it was held between the colonists and was not 'a trial of ploughs by experts'! The total area then under cultivation was reported by McKen as not exceeding four acres because the means at his disposal were very limited and this restricted the amount of bush that could be cleared.

EARLY SUGAR INDUSTRY IN NATAL

McKen had considerable experience in the growing of sugar cane prior to his arrival in South Africa, having worked on the Golden Grove Sugar Estate, Port Morant, in Jamaica from 1840 to 1849. It is not surprising, therefore, that he played an important part in the birth of the sugar cane industry in Natal.

Sugar-cane had been known to occur here before the advent of Europeans, because the earliest record was of some shipwrecked mariners who in 1635 discovered natives near Umzimkulu growing cane amongst their other crops. In the early days of the colonists cane was found to be grown in small quantities about the kraals of chiefs. Edmund Morewood was first in growing cane on a commercial basis and, together with other canes imported from Mauritius in 1847, he provided the foundation of the sugar industry. It was originally thought that the cane found in Natal was indigenous but according to Dr A. McMartin, ex Director of Mt Edgecombe Sugar Research Station, 'The sugar-cane plant has a very long history in Central and East Africa, having been known in the twelfth century on the East African coast. The chief agents in its introduction were the Arab slave traders in the Lake regions and early Portuguese explorers along the Zambezi. It then became widely disseminated by the Africans as garden canes'. It appears the cane is Indonesian in origin and probably entered Natal via Mozambique. To distinguish the local cane from the imports, Morewood called it Green Natal and it was to form the basis of the industry until 1870.

McKen visited Morewood at Compensation Estate in May 1852 together with a party of other 'big names of the young colony' to discuss the general capabilities of the colony as a field for immigration with special reference to sugar planting and tropical agriculture.

Later McKen reported to the Natal Agricultural and Horticultural Society on his findings (Osborne, 1964). While at the farm for two days he had extracted sugar from two of the varieties and recorded the production of juice per weight of cane used. A description of how this was done is given by J. F. Hirst: 'Implements employed in the manufacture of sugar being a pair of wooden rollers hewn from an old mast, for crushing the canes and an ordinary kafir cooking-pot of about three gallons capacity for boiling the juice'. McKen ascertained the densities of the liquids and the amounts of cured sugar and molasses produced. He concluded that 'the canefields at Compensation, if properly attended to, would produce a profitable return: both soil and climate being peculiarly adapted for the growth of the plant'. This was an important report, because the resolution passed by the group was that they had 'full confidence in the capabilities of Natal as being not only equal but in many respects far superior to the island of Mauritius'. Sugar then began to attract interest, although Morewood ran into financial difficulties and had to sell out and emigrate to Brazil.

DURBAN BOTANIC GARDENS 1853–1872

On 9th July 1853 McKen resigned as curator of the Gardens to become Manager of Messrs Chiappini's sugar estate at Tongaat. A quick succession of curators followed by whom very little work other than garden maintenance appears to have been done: Alexander Smith from 5th August 1853 to July 1854, Robert William Plant, August 1854 to July 1856, Jasimir Weir, July 1856 — July 1857, R. Rogers July 1857 — notice given in 1859, De la

Chaumette, 3 months trial in May 1859, and A. Moore, May 1859 to September 1860. The Society then approached McKen and prevailed upon him to resume his position in the Gardens at an increased salary of £150 per annum. He agreed and started officially again in December 1860. During this period attention was paid to the introduction of economic plants other than food crops. Bamboos, Australian gums and other timbers were propagated and many purely ornamental plants were introduced, such as palms, foliage plants and flowering trees and shrubs.

McKen was an enthusiastic botanist as well as horticulturalist and he collected extensively in the coastal and inland areas of Natal. He also collected between 1862 and 1865 with an English naturalist, William Gerrard. The originals of these went to Kew via Cambridge, but the duplicates, together with McKen's own collections, of which some 500 specimens remain today, were to provide the basis for the Natal Herbarium which was established by John Medley Wood in 1882. McKen was particularly interested in ferns and he published a small booklet on *The ferns of Natal* in 1869, and, with Gerrard, the *Synopsis filicum capensium* in 1870. Gerrard contracted fever during his collecting trips and died in 1866 in Madagascar. The majority of the plants collected by the two men were new to science and both are commemorated in the scientific names of many of these plants.

During the whole of his term of office, McKen corresponded with Kew and other important botanical and agricultural stations in various parts of the world. In exchange for seeds and specimens of our indigenous plants, he obtained a great variety of interesting plants for the Gardens, many of which are still in existence today.

Gardening operations were carried out under serious difficulties in those days. All the water used was carried from a well at the bottom of the Gardens and, during the periodic droughts which occurred, many valuable plants were lost. Several complaints are recorded about the quantities of mud, tadpoles and mosquito larvae in the drinking water supply. The latter in their mature form still represent a menace at the herbarium today. McKen died on 20th April 1872 from yellow fever and a kidney disease and the following is recorded in Osborne: 'His loss was felt keenly enough but when 96 new varieties of cane arrived from Mauritius for propagation, his absence was greatly deplored'.

JULIUS WILHELM KEIT

While the post was vacant, first Mr Steel and then Mr Thomas Ridsdale, members of the committee, took charge of the Garden from April until the arrival of the new curator, Julius Wilhelm Keit, who assumed curatorship on the 14th November 1872. A Dresden-trained horticulturalist, he was employed at the Royal Botanic Garden, Glasnevin, Dublin, when on the recommendation of Sir W. J. Hooker at Kew, he was appointed to succeed McKen. He held the post for what appears to have been a difficult ten year period with little money or facilities for development. The Society did not have the funds to improve the Garden and the sale of plants was the major source of revenue. Experimental work was still being done and trials with Ceara rubber were proving very satisfactory in 1880, although no success had been achieved with *Hevea brasiliensis*, the all important rubber-producing tree of the present day. His major interests were sea algae, palms and cycads and in December 1881 he resigned from the Botanic Gardens mainly because of the financial situation, to take up curatorship of the gardens of the Durban Municipality. He continued here until his death in 1916 and is responsible for planting the coconut palms along the esplanade, creating the Victoria and Albert Parks and laying out the gardens around the Town Hall. He owned his own nursery and supplied plants to the borough from this.

About the time Keit resigned, a definite break had occurred between the Natal Agricultural Society and the Horticultural Society and so at an urgent meeting it was resolved to ask the Government to help finance the Garden. This was granted with the formation of the new Durban Botanic Society. This body assumed control of the Botanic Gardens and continued to do so until it ceased to function in 1913.

JOHN MEDLEY WOOD

Prior to his appointment as the next curator on the 1st March 1882, John Medley Wood had been a successful farmer and trading store owner in Inanda. At the age of 24 he joined his parents, who had earlier emigrated to South Africa and, during the intermediate years, he farmed first with arrowroot and, when the price fell, he switched to sugar cane, coffee and castor oil.

From an early stage he had a consuming interest in botany and widely collected cryptogams, fungi, ferns and mosses as well as flowering plants. He built up extensive connections with local and foreign botanists sending large amounts of specimens to Kew and receiving many in exchange. At the time McKen was working in Tongaat he met Wood and later married his sister, Margaret Wood. In 1855 Wood married his stepmother's younger sister, Elizabeth Haygarth. Wood's interest in ferns led to his first publication in 1877, *A popular description of the Natal ferns*, followed in 1879 by *The classification of ferns*. He was assisted in this undertaking by Rev. John Buchanan, who was in Natal from 1861 to 1874.

A clergyman originally from Scotland, Buchanan set up the Presbyterian Church in Durban and Pietermaritzburg. He visited many mission stations and, because of his interest in grasses and ferns, he collected widely in Natal. In 1875 he published *A revised list of ferns of Natal* and some 570 of his specimens are preserved in the herbarium today.

ORIGINS OF NATAL HERBARIUM

Wood writes: 'On becoming the curator of these Gardens, my first and most important object in view was that of starting an herbarium, for without one the name of Botanic Gardens was not justified. An herbarium means in reality a dry garden, a garden that in a few minutes can be consulted by a botanist like a dictionary'. He inherited a small collection of some two thousand specimens chiefly those collected by McKen and Gerrard, but some also from Australia and Syria. These were housed in a wood and corrugated iron building which was in very poor repair and the specimens were badly damaged by termites and rats, so he saved what was still of use and classified and named them. In his highly informative *Reports on the Natal Botanic Gardens and Colonial Herbarium* (1882–1910) he states:'The Herbarium belonging to the Gardens is not in a state which renders it of much use to the student. The specimens are unmounted and old newspapers supply the place of both species covers and genus covers. So far, I cannot say the herbarium has been consulted by anyone but myself, only two persons have expressed any desire to see it'. At the same time he had his own collection housed in a separate building. Two self-made cabinets contained his collections, chiefly from Inanda, (1500 specimens), 200 American plants from Mrs Edwards of the seminary in Inanda and a large parcel of plants as a donation from Kew. The duplicates of his collections brought for the purpose of exchange were donated to the herbarium at the Gardens.

Although curator of the Gardens, Wood had no training in horticulture so in June 1882, when James Wylie who had been trained at Kew arrived, he was employed as gardener under Wood. This era now marked the beginning of a new phase in the development of the Gardens which was run along more generally accepted botanic garden lines and the agricultural aspect was dropped. New plants of all types were added to the collections, but the majority of introductions were ornamentals. Wood built up an extensive seed and plant exchange network and he was always ready to give help and advice to the farmers and horticulturalists on any subject to do with the culture of plants or on their diseases. He was also consulted about many pest and insect problems.

From the beginning he collected extensively making annual trips by oxwagon to various parts of Natal and Zululand. He added numerous new records to the flora of Natal and his name is now commemorated in the scientific names of many of our Natal plants.

WOOD AND THE SUGAR INDUSTRY

The sugar industry had flourished along the Natal coast and by 1870 another variety called China cane had superseded Green Natal as the major producer. However, in 1889, a blight disease caused by the smut *Ustilago sacchari* wiped out most of the popular varieties and it was fortunate that, through introductions of imported canes during the preceding years, one emerged to save the industry from virtual extinction.

Who first introduced Uba cane to Natal is not clear, but there are two likely possibilities. Mr Daniel de Pass, who owned an estate along the south coast, communicated with a number of sugar estates around the world and obtained varieties of cane from Egypt, Louisiana, Mauritius, West Indies and India.

These were all planted on his Reunion estate when they arrived in 1884–1885. The last box to come was left carelessly underneath some sugar bins and was discovered only some time later. The box contained cane tops and, luckily, some had managed to survive. In trying to trace a label for the cane they could only make out the letters 'Uba' badly written on the box and so it was called by this name. It is believed that most of the Uba cane grown along the south coast arose from this original stock. However, another story closer to home is put forward to account for Uba introduction north of Durban. Osborne writes about the same time, 'Governor Mitchell arrived from India with two Wardian cases of cane plants which he gave to Medley Wood for attention. Only three plants were found to be alive but the Curator propagated them successfully giving the results to Anthony Wilkinson of Ottawa Estate'. Here it was hazarded that 'Uba' was part of the name 'Boubaya' — a Madagascan cane. Whatever the real origin, it appears that Uba is not a fortuitous name as it is also known by this name in Jamaica and Australia. The real advantage of Uba cane was that it withstood the Natal climate better than others and was resistant to the locust and fungal attacks that beset the other types. After 1890 Uba cane became the backbone of the sugar industry when the other varieties failed.

DEVELOPMENT IN THE HERBARIUM 1885–1900

By 1885 considerable interest had been shown by the colonial government and the Directors of Kew in the development of the Herbarium. Sir H. E. Bulwer visited the gardens in this year especially to inspect the herbarium and to see what was being done there. The result was, as Wood states, 'His Excellency was good enough to forward a cheque for forty guineas for the purchase of a first class microscope for use in the Herbarium'. In addition, the contents, but not the building, were taken over by the Government and it became known as the Colonial Herbarium from this time. At this stage the collection consisted of nearly 2 500 South African and 900 foreign specimens.

In 1886 the Government made a grant of £67 13s ld to the Curator to be used for mounting specimens and for cabinets to house them. It was also for the purchase of botanical books and periodicals. Six cabinets were obtained each with sixteen compartments and the books, together with Wood's private library, were to be the start of the excellent collection housed at the Herbarium today. A £30 grant was made annually hereafter for the purchase of more books.

1888 saw the publication of Wood's *An analytical key to the natural orders and genera of Natal indigenous plants* and in 1889 the herbarium gained a significant contribution of specimens from Harry Bolus. Today there are nearly 1 300 of his specimens in the collection. Wood writes: 'Finding it most inconvenient to have to consult two separate herbaria, situated in buildings far apart from each other; I have transferred a number of the specimens from my own herbarium to the cabinets of the Government Herbarium, many of them being rare and valuable specimens. I may never wish to resume possession of them again; but if at any time I should require them it will be easy to separate them, as the larger portion are still upon the original sheets with my own private stamp upon them, over which I have placed the Government stamp and number'. He actually transferred all his specimens and his own cabinets to the Government Herbarium at a later stage.

In July a bazaar was held in the Durban Town Hall under the direction of the Botanic Society for the purpose of raising funds for the erection of a residence in the Gardens for the Curator, the house in which he had lived hitherto, the oldest house on the Berea, 'having become dilapidated and almost uninhabitable'. To this bazaar was sent, in pots and tubs, 838 plants, 588 for sale and 250 for decoration, 6 hanging baskets and 5 window boxes filled with plants. Of these, 274 were sold realizing about £40 which went to the bazaar fund. This was the contribution of the Botanic Gardens. When the bazaar and closing concert were over and all the expenses were paid, a total of £758 had been collected. The balance needed to pay for the house was obtained by private subscription and the contractor started work on September 16th, though progress was delayed due to the difficulty in obtaining workmen and carts for delivering bricks. The house was finally completed in July 1890 for the grand total of £1147 1s 5d.

In his report for 1890 Wood says of his new house, 'It is well built and ornamental and I think reflects much credit on all those who were so energetic in procuring the funds for its erection. After the old residence had been evacuated by the Curator's family the hands were employed for some time in pulling it down and removing the materials which are now available for erecting a new store, tool house and potting shed which are much wanted'.

This first house (Fig. 2) on the site of the present Herbarium complex is still used as the administrative office today.

By 1891 H. Rutter was employed to bolster the staff of the Gardens and Wood was finding it difficult to cope with the growing herbarium on the slender funds granted to him. He notes there was a shortage of bookcases and herbarium cabinets and that the annual grant of £30 was inadequte. In 1894 Wood published *A primary catalogue of indigenous Natal plants*. By 1895 the collection had grown to over 17 000 specimens of which 7 300 were South African.

The Government grant was raised to £100 per annum which allowed Wood to obtain the services of a half-day assistant, Miss Lauth, who started in July. From March of the following year Wood was able to employ Miss Lauth full-time and, besides helping with general curating of the collection, she did botanical illustrations on the herbarium sheets, particularly dissections and sketch drawings of the Gramineae. At the same time, Maurice Evans, a businessman and politician, who was later to become MP for Durban in 1906, helped Wood in his spare time with work on the indigenous flora. He collected extensively in the Drakensberg bringing back many new records and he published, jointly with Wood, the first of the latter's 6 volume series of illustrated *Natal plants*. He collected about 800 specimens for the herbarium from Natal and Zululand between 1894 and 1897. Another person who contributed a number of illustrations for Wood's work was the artist Walter Haygarth, Wood's adopted nephew, and he collected some 200 specimens from Natal and the eastern Cape.

A NEW HERBARIUM BUILDING

By 1900 the herbarium collection stood at 26 000 with nearly 8 700 South Africans plants, and these were all housed in 34 cabinets. In his report for this year Wood calls attention to the fact that the iron and wood-lined building which housed the collection was owned by the Botanic Society and was urgently

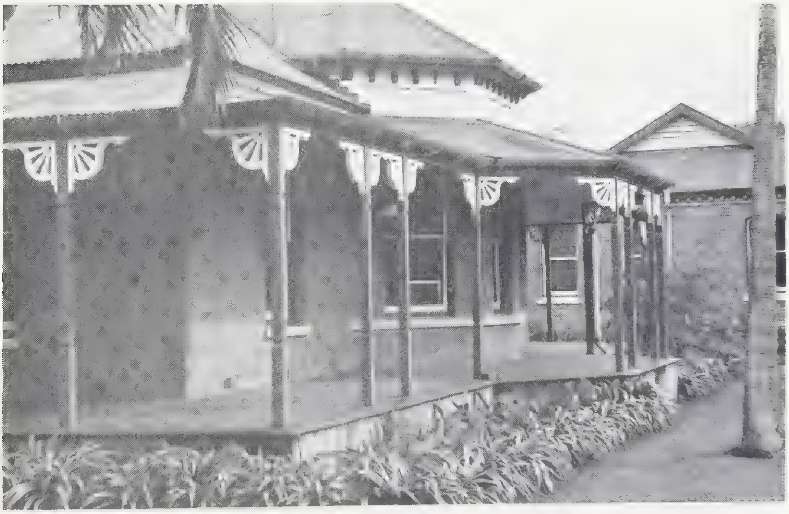

FIG. 2.—Medley Wood's house completed in 1890 and now used as the administrative office. Photo: J. Reyburn.

required for other purposes. Besides, the building was too small and in great danger of fire particularly from the spirit lamps that were used. It was also subject to all sorts of insect attacks. Application was made to the Government to provide a suitable new brick building for the herbarium. Wood writes 'I was deputed to meet the Premier in Pietermaritzburg on the subject. I took a ground plan of the proposed building drawn out by myself and put into form by my nephew Mr Haygarth'. The plan was submitted by the Premier to the Public Works Department, which estimated the cost at around £1 600. The Premier agreed that funds could be provided and Wood was authorized to call for tenders. When these were received, the lowest was £2 200. The Government finally agreed to this and the reasons given for the differences in estimates were the sloping character of the ground and Wood's insistence that the walls and foundations be strong enough to enable another story to be built on at a later date. He envisaged the development of a Technological Museum on the lower floor with the herbarium above. Although this idea never came to fruition, much of the material he collected forms the basis of the museum at the herbarium today. Work started on the building on December 5th 1901 and it was completed in the following year (Fig. 3). An additional £200 was placed on the estimates for furniture and fumigation of all specimens before being transferred into the new building.

In November 1901 Miss M. Franks was employed as botanical artist and assistant to Wood and she did most of the illustrations from Volume 3 onwards of *Natal plants.* She also contributed plates for Marloth's *Flora of South Africa* and collected some 370 plants from Van Reenen, Camperdown and Durban.

By mid-1903 the collection had grown to nearly 29 000 housed in 41 cabinets. Volume 4 of *Natal plants* had been completed and Wood writes: 'I am glad to say that the building is commodious and, better than that, it is from its height above the ground and the asphalt platform on which it is built, quite dry, so that the specimens are not in danger of damage from damp'. Miss Lauth left in 1903 after also drawing a number of plates for *Natal plants* and in 1905 Wood became the Director of the Gardens and Colonial Herbarium. Wylie was made Curator of the Gardens until his retirement in 1916, but he continued collecting after this and over 1000 of his specimens are now housed in the herbarium. In 1907 Wood published *A handbook of the flora of Natal.* At this stage funds were markedly reduced and the services of a junior assistant had to be dispensed with.

In Wood's last report in 1910 the herbarium contained nearly 43 000 specimens, 12 500 of which were South African. Funds were still a problem, but a grant of £35 made it possible to begin Part 2 of Volume 6 of *Natal Plants* which was completed only in 1912. In February 1913 Wood was awarded an honorary D. Sc. degree *in absentia* by the University of Cape Town.

NATAL HERBARIUM TRANSFERRED TO UNION GOVERNMENT

In the same year the Botanical Society, which had been suffering through a lack of funds, finally split the property, donating the two acres on which the herbarium stands today to the Secretary of Lands in the Union of South Africa. It was then transferred to the newly-formed Government Division of Botany and Plant Pathology under Dr I. B. Pole Evans. The rest of the Gardens was transferred to the Townlands of the Borough of Durban.

Wood retired from the Gardens but still remained in charge of the Herbarium as Director. Miss Franks left at the end of 1914 and was replaced by Miss K. A. Lansdell, who prepared the plates for the incomplete and unpublished Volume 7 of *Natal plants.* She also completed a number of plates of Natal plants in watercolour which today hang at Natal Herbarium. She moved up to Pretoria in 1917,

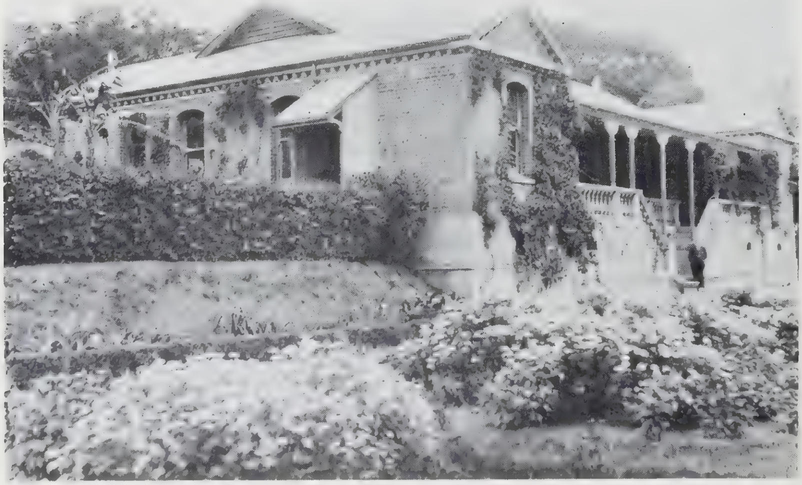

FIG. 3.—The Natal Herbarium built in 1902.

where she contributed many plates for the first volumes of *Flowering plants of South Africa.*

DEATH OF WOOD

John Medley Wood (Fig. 4) died on 26th August 1915 at the age of 87 in the house that was built for him as curator of the Botanic Gardens. He had built up, over 33 years, a herbarium with a world-wide reputation. He initiated a large scale exchange programme which led to the incorporation in 54 cabinets of nearly 30 500 extra African and over 2 000 tropical African specimens and he had also accumulated 13 500 South African plants, all of which were entered numerically and indexed for ready reference. It is unfortunate that, through this exchange, only 6 000 of his total collection of 13 099 remain at Natal Herbarium, the rest having been sent overseas and to other herbaria in South Africa. Through his contacts he was able to build up a most comprehensive library and much of his furniture and effects collected over the years are in the museum here.

It should be remembered, though, that the herbarium was part of the Botanic Gardens and it was the combination of the two that gained its reputation under the Directorship of Wood. After the split in 1913, both declined in influence and in the words of F. W. Thorns, a past curator of the Botanic Gardens, 'The loss of the herbarium made the Gardens very like a cart without a horse, and it soon lost its status as a botanical institution to become, in effect, a public park'. The herbarium, too, slipped into obscurity and for nearly 50 years the emphasis lay on plant pathology.

In the annual report of the Department of Agriculture for the year ending March 1913 reference is made to the acceptance by the Department of the Natal Herbarium from the Durban Botanic Society. A decision was made to maintain the herbarium in Durban and also to enlarge the scope of the station as a research centre for the investigation of diseases of tropical and subtropical crops. In the clause, however, the herbarium was handed over on the condition that it was not to be moved from Durban and that it was properly looked after.

BOTANIC STATION AND PLANT PATHOLOGY

The first mention of a plant pathologist becoming involved with the herbarium was when Dr P. A. van der Byl from Pretoria visited Wood in 1914. An Indian assistant and long-standing plant collector for Wood, Moonsamy, was working here at the time. He is heard of again and was pensioned off in 1928. 1914 saw the building of the present labourer's quarters for £125.

On the death of Wood, Van der Byl was transferred to Durban in September 1915 as the first Mycologist in charge of the Botanic Station. Wood's house was converted into a laboratory chiefly for the study of fungal and bacterial diseases and work consisted of giving advice to the public and doing research. Van der Byl worked particularly on those diseases affecting citrus and other subtropical crops, but there was also considerable interest in the diseases of fibre plants. Wood had pioneered work on indigenous fibres and his collection of samples of the fibres of many Natal plants, together with various indigenous dyes, are now housed in the museum. Van der Byl also acted as botanist providing a routine identification service.

FIG. 4.—John Medley Wood (1827–1915).

In 1913–1914 the Natal Sugar Association obtained a piece of ground on the Eastern vlei (where Kingsmead stands today) to be used as a quarantine experimental station for new varieties of cane. Planting began in 1914 and this was done under supervision not only by the sugar industry but by the Government pathologist, entomologist and sanitary inspector. The entomologist at this time was C. P. van der Merwe who was based at a small office at the Point. The first issue of these canes came in 1916 and specimens were sent to Natal Herbarium. Valuable research into the fungi causing deterioration of sugar in storage was carried out by Van der Byl, as well as investigation into several other cane diseases. He also built up a very large collection of fungi, particularly bracket fungi and toadstools found on tree stumps, which provided the basis for a mycological herbarium.

The first batch of canes released from the quarantine station included some varieties from Argentina. Ironically, it was these that were later identified as having been infected with mosaic disease, and it was the control of this disease which occupied most of the research done at the Botanic Station for the next twenty years. Mosaic was first observed in 1918 and by 1923 it had spread so extensively that all soft cane and Argentinian varieties were infected. Uba cane, (alone), was free from it. Later, however, a second devastating disease called streak ravaged Uba and most other varieties as well.

THE STATION EXPANDS 1919–1929

On 1st July 1919 Miss Helena M. L. Forbes was employed at the station as botanical assistant in the herbarium and she gradually took over its maintenance and the identification service of plants. She soon became involved in research and in 1920 revised the genus *Cassia* for Natal as well as preparing *The flora of Isipingo* and *The flora of the Malvern district.*

During this period the entomologist in Durban had been seeking an office at the station and subsequently he moved to an old shed just below the herbarium. There was talk of erecting a new office near the entrance for him so that it could be accessible to the public, but in 1921 Van der Merwe moved into the herbarium building instead and occupied the museum room there.

Plant inspection of the imports and exports of live plants and fruit and fumigation of sugar cane cuttings was carried out at the Point by a plant inspector who was supervised by the emtomologist. R. H. Harris was inspector until January 1921 when C. C. Kent was employed to replace him.

In June 1920 J. Reyburn was taken on as general lay assistant at the station doing mostly clerical, photographic and maintenance work, while assisting the Mycologist or in the herbarium.

In June 1921 P. A. van der Byl retired from the civil service taking up the appointment of Professor of Phytopathology at the University of Stellenbosch. Dr H. H. Storey became the next mycologist in charge and he was responsible for pioneering work on plant virus diseases in South Africa. His major concerns were mosaic and streak in sugar cane as well as streak disease in maize and rosette in groundnut. To control mosaic in sugar cane, he introduced a campaign for the destruction of old susceptible varieties which were scattered throughout the cane areas. This idea had to be abolished later after Storey discovered that the wild broad-leaved grass *Setaria megaphylla* acted as a reservoir for mosaic, and the aphids feeding on it would continually reinfect the cane. The only solution was to grow sugar cane that was immune or highly resistant to the disease. The monitoring of the spread and control of sugar diseases necessitated the employment of a small staff of disease inspectors. The first of these were Levitt and MacKay and their routine was to travel up and down the Natal coast reporting back to the mycologist onhthe overall situation. Storey was also responsible for the advisory workmon plant diseases in Natal.

In 1923 Miss Forbes started work on the revision of the genus *Psoralea* and an artist, Miss Gower, was employed for a while to paint and help prepare mosaic disease infections for research. During periods when Kent was on leave, Reyburn carried out the plant inspections at the Point, one of the products demanding attention from this time being seed potatoes.

1924 saw the establishment of the Sugar Research Station at Mt Edgecombe, while in June of this year Storey mentions that the rooms occupied by the Natal Entomologist were urgently wanted by officers of the Division of Botany and Plant Pathology to provide room for more technicians to investigate pineapple disease in sugar cane. The entomology buildings was then erected by the Public Works Department in 1925–1926 for £1632 and this third building placed behind the herbarium completed the facilities presently available at the station. As a result of the need for more staff, a scientific assistant post was created for the mycologist and Mr R. F. W. Nichols was employed in January 1925. The post was filled on and off until 1963 when Plant Pathology left the station. Miss A. M. Bottomley from Pretoria assisted Storey for a while. In 1925 the herbarium collection had increased to 17 689 specimens.

In April 1926 the Sugar Research Station opened a new Quarantine Greenhouse which they built at Natal Herbarium. Storey writes in an article published about the new greenhouse, 'The import of plants from foreign countries involves great risk of the introduction of new pests and diseases. Especially is this true when the plants are grown from cuttings and not from seed. Sugar cane is, therefore, a particularly dangerous plant to import without due precautions; and the majority of the serious outbreaks of disease in different cane-growing countries have been caused by the accidental introduction of disease in imported cuttings'. It goes on to say, 'It has recently become plain that the growth of imported cane in quarantine stations located in the open affords insufficient security, since it involves a risk that diseases may become disseminated before their recognition. It was to evade this danger that the construction of a quarantine greenhouse now erected at Natal Herbarium was deemed to be necessary.' The greenhouse was handed over to the custody of the Government Mycologist and considerable research at the Botanic Station resulted in the introduction of many new varieties of cane to the industry. The quarantine greenhouse is still used today but it is administered entirely by Mt. Edgecombe.

To emphasize the importance of the pathological work being done at Durban, another mycologist Dr A. P. D. McClean was transferred from Pretoria to the Botanic Station in mid-1926. He and Storey worked together until February 1928 when the latter left to go to the Amani Research Institute in Tanganyika. McClean then became the next mycologist in charge. Dr Storey (Fig. 5) was considered a very capable and brilliant research worker and he published prolifically. The number of sugar disease inspectors had also been increased with the employment of Sinclair and the seconding of R. H. Halse from citrus canker in late 1927.

The Division of Entomology was joined with Botany and Pathology under I. B. Pole Evans and it was about this time that the entomologist C. P. van der Merwe was transferred to Pretoria, because it was felt that the work in Durban did not warrant the post. Kent remained in the entomology building as plant inspector and assistant entomologist and from

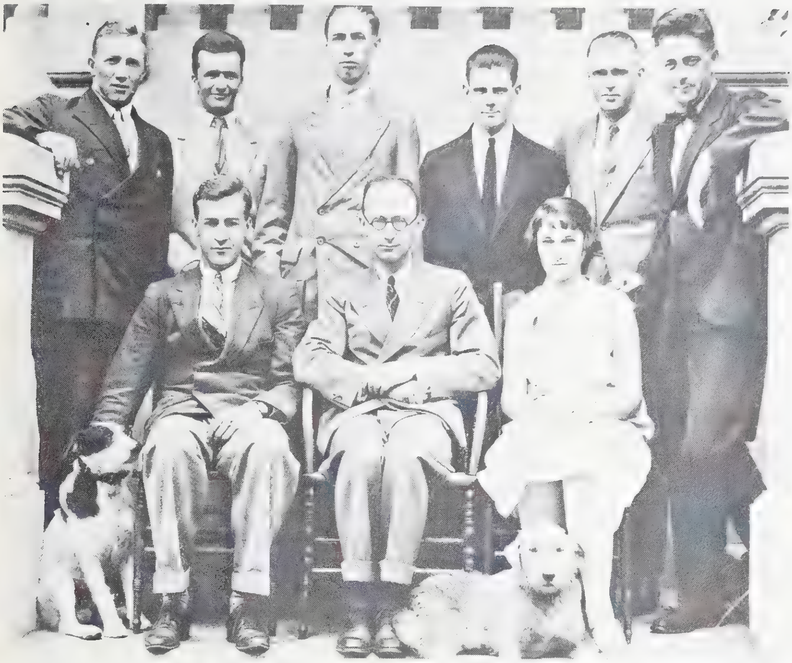

FIG. 5.—Staff of the Botanic Station, Durban, in 1927. Standing (left to right); Mr R. H. Halse, Mr D. Sinclair, Mr R. F. W. Nichols, Mr J. Reyburn, Mr J. S. Mackay and Mr C. Kent; sitting: Dr A. P. D. McClean, Dr H. H. Storey and Miss H. M. L. Forbes.

this period the mycologist answered most queries on entomology referring the problems often to Cedara or Pretoria. Kent remained under the supervision of Van der Merwe who returned to Durban in the thirties when phytosanitary considerations increased in significance, but he was then stationed at the Point office. In the herbarium, work was being done on a revision of the Umbelliferae. In March 1928 inspector Levett resigned and R. H. Halse was employed permanently in his place.

Dr McClean continued the work on plant virus diseases, particularly streak and mosaic in sugar cane and maize, mosaic in wild grass hosts, rosette and bacterial wilt in peanuts, bunchy top disease of tomatoes and leafcurl in tobacco. Attention was directed to a study of the methods by which the diseases were transmitted, the hosts of the causal viruses, the reaction of the susceptible hosts and the possibility of utilizing varietal resistance as a method of control.

The lay assistant appointed to the mycologist was involved in planting seeds, supervising sterilization of the soil, planting out seedlings to use in experiments, spraying and estimating and counting amounts of disease present under treatments. The facilities available for research included a laboratory equipped for study of plant diseases (fungus, bacteria and virus), the insect proof quarantine greenhouse which was used to study insect virus diseases and special insect chambers of various design to study the same.

DIVISION OF PLANT INDUSTRY

In 1929 the Division of Plant Industry was formed comprising the sections botany, plant pathology, horticulture, entomology, field husbandry and pasture research all under the directorship of Dr I. B. Pole Evans. Miss Forbes's revision of *Psoralea* was published in 1930 and by the end of the year R. H. Halse was the only sugar inspector remaining at the station.

From June 1931 arrangements were made for Kent to move from the Botanic Station to the Point, although the entomology building remained a subsidiary office and two rooms were used as the library. Besides inspecting all produce at the harbour, Kent had to go up to Pietermaritzburg regularly to inspect nurseries for pernicious scale. Plants, bulbs etc had to be fumigated in a cyanide gas chamber before they were allowed to be planted. Reyburn continued to help Kent when the latter was away on leave. In 1931 it is recorded that there were 457 books in the library and 500 volumes of periodicals.

Up until 1933 clerical work and typing had been done by one of the lay assistants, usually Reyburn. On 1st December Miss Hessom was transferred to the station from the cotton graders office, as a temporary clerk, chiefly to take over clerical work, although she helped in the herbarium as well. This new post has been filled with short interruptions up to the present day. In 1933 Dr A. McMartin joined Mt Edgecombe as botanist and found that nearly all research work on sugar diseases was being done at Natal Herbarium. Since the emphasis was on viruses here he began work on fungal diseases at Mt Edgecombe. Dr McMartin later became Director of the Experiment Station.

In 1934 Miss Forbes began her revision of the genus *Tephrosia* and in 1935 six new cabinets were added to the herbarium. At this stage the collection of South African plants had grown to 26 606 with the inclusion of a large number of Thode specimens. There are now over 3 000 of these in the herbarium. Another collector, Rev. J. Gerstner, also comtributed a large number of specimens collected from Zululand and northern Natal.

On 13th November 1935, Reyburn left the station on transfer to Pretoria and Mr R. H. Shears replaced him as general lay assistant. In May 1936 J. C. Howlett was transferred from Pretoria as a botanical assistant to help in the herbarium, while Miss Forbes went to Kew as South African liaison officer. Howlett was not a qualified botanist, but he looked after the curatorial side, doing mounting and pressing as well as helping elsewhere. In 1937 Shears resigned and it appears that the post of general assistant fell away. On 1st August Miss B. M. Ogilvie, a graduate botanist from Natal University, was employed to take over the identification service of the herbarium.

Another glasshouse was erected by the Division of Plant Industry in 1937 for £830 and it was used by the plant pathologist until 1965 when it was demolished.

DIVISION OF BOTANY AND PLANT PATHOLOGY

In January 1938 investigations were made and reports submitted in order to improve the staff situation in the herbarium and to promote research there. Accordingly, in June 1939 Dr H. G. W. Schweickerdt, a taxonomist, was transferred from Pretoria to Durban. He undertook research into the genera *Aristida, Tragus* and *Dactyloctenium* and added a considerable number of specimens to the herbarium particularly those of Volk and Dinter. At the end of September Miss Ogilvie was transferred to Pasture Research and in November Dr J. A. Payn from Natal University replaced her in the herbarium. In this year Pole Evans retired and the Division of Plant Industry broke up again into its separate divisions with Dr E. P. Phillips becoming head of the Division of Botany and Plant Pathology.

1940 saw some considerable changes in the Botanic Station as the effect of World War II began to be felt. Dr Payn resigned in April and in July R. H. Halse went on active service. Dr V. A. Wager, who had been awarded a Commonwealth Fellowship to California for two years, returned to Pretoria and was transferred to Natal in September. He was to replace McClean who had indicated that he would be leaving on active service shortly. By this time, work on sugarcane had ceased, as the Experiment Station at Mt Edgecombe took on all disease work in this field. Miss K. Lansdell returned to the herbarium in retirement to paint until leaving in 1943. In October 1940 Dr Schweickerdt left the station to be interned. The entomology building was again used for a short time by Captain Putterill of Defence who used the fumigation chamber and storeroom there as incubation rooms for the observation of certain canned foods.

Miss Forbes returned to Natal Herbarium in July 1941 after a period at the National Herbarium in Pretoria, where she had worked on her return from Kew. Together with J. C. Howlett, they continued to run the herbarium which by this time contained 33 840 specimens. On 1st July McClean left on active service and Wager took over as acting mycologist in charge pending his return. All the type specimens which had been sent to Pretoria during the war were returned and filed in 1944 and three new cabinets were installed. R. H. Halse came back in December from a prisoner of war camp at Tobruk and Dr R. A. Dyer succeeded Dr Phillips as head of the Division.

1945 saw the split of the Department of Agriculture and Forestry and a further three new cupboards were placed in the herbarium. Dr McClean returned briefly in June 1946 to be transferred almost immediately to Pretoria and Wager officially took charge of the Botanic Station. He was involved in a lot of extension and field work giving talks to farmers and garden clubs and dealt with a large amount of correspondence, being the only pathologist in Natal. Most of his time was occupied in research on black spot in citrus, rust disease in *Gladiolus* and *Antirrhinum* and anthracnose in pawpaws. Research was also done into vegetable diseases especially bacterial wilt and bacterial canker in tomatoes. Field experiments were carried out in the Underberg area to increase the yield in potatoes. Results of most of this work were published in Government bulletins and scientific periodicals. The disease inspectors were still employed by Plant Pathology and in 1947 H. V. Frances joined Halse for inspections.

TIMBER CONTROL OFFICE

In 1948 Mr K. Bock was transferred from Pretoria for a while to help Wager with black spot disease in citrus and 1949 saw a new development in the third building where the Division of Entomology established a Timber Control office. A report in the Daily News in October 1947 read: 'The Union Government of Entomology regards it in the national interest not only to stem the tide of damage done by termites in Durban, but to prevent the spread of their ravages into the interior which may be more favourable to the pest than first thought. Officers recently sent to Durban to investigate the situation had made a report on the campaign to be used to control the pest. It was suggested that timber passing through the docks in Durban was greatly endangered. The termite is a slow working insect and timber moves through fairly fast. *Cryptotermes brevis* differs from other termites in that the whole colony lives sealed up inside the wood. They have been known since 1921 where the original infestation was found in an office desk. On later investigation it was found that the termite was already widespread'. In fact, it is believed that *C. brevis* entered Natal in a consignment of timber around 1918. A sample of the insect was sent to America for identification, but was wrongly named and thought to be harmless. Another American, Emerson, later positively identified it, but by then it had become established.

The first Timber Control officer to be based at the Botanic Station was C. C. van Zyl in November 1949 and the work included inspection of all imported timber yards. Secondhand furniture, demolitions where timber was to be used again, alterations and additions to buildings involving wood and consignments of secondhand timber all had to be checked. Many calls and queries from the public were answered here and eradication work and the treatment of buildings by private firms had to be supervised. The work required a large staff and C. Kent was brought back to the station, and other plant inspectors were employed. In March 1951 Van Zyl died and was replaced by J. L. de Goeda who was transferred up from the Cape. The normal inspections of plants, fruit and potatoes, fumigations, and issuing of import permits and phytosanitory certificates were also handled from this office. By 1950 the herbarium collection had grown to 39 960 with large contributions by Acocks, West, Lawn, Schelpe and Fisher.

J. Reyburn was re-employed again for eighteen months in May 1951 but as an assistant to the mycologist this time, and J. C. Howlett, who worked for 14 years as botanical assistant at Natal Herbarium and who contributed over 300 specimens to the herbarium, retired on pension in February. The post of technical assistant in the herbarium, often shared with Plant Pathology initially, has been maintained ever since.

DIVISION OF BOTANY

In 1953 large organizational changes occurred within the Department of Agriculture and most outstations were transferred to regional control in a move towards decentralization. The separate Divisions of Botany and Plant Pathology now came into being; the former, to which the Botanic Station was transferred, remained centrally administered from Pretoria with Dr Dyer as Chief while the latter became regionalized. Dr Wager remained at the station as a senior officer in the region because of his specialist knowledge of plant diseases in the coastal area, but Miss Forbes now became officer in charge of the station. On 5th January Miss A. Dohse was transferred from the National Herbarium in Pretoria to help Miss Forbes who had been ill for some time with rheumatoid arthritis. The Division of Entomology which had until now contained a section called Plant Regulatory Services also split in this reorganization with the latter becoming known as Plant Control and Quarantine. It was to this division that the timber control work at the station belonged. In the same year C. Kent, who was already a pensioner, was transferred to East London and G. P. Botha continued as plant inspector.

The next few years saw the largest turnover of staff in the stations history. On the 10th October 1955 Miss H. M. L. Forbes retired unable to continue working through illness and she died in 1959. She had contributed over 1 400 specimens and in 36 years of service had been, 'the stalwart that kept botanical wheels turning at the herbarium'. Miss A Dohse became officer-in-charge from this date and on the 14th November Miss. S. M. Johnson, Senior Professional Officer was transferred to Durban from the Albany Museum at Grahamstown.

In the same year, J. L. da Goeda left as Timber Control Officer and was replaced by Mr T. H. Marincowitz; and there was a large reorganization of Plant Control and Quarantine in Durban. Halse and Frances who had become attached to this Division left the station for the Indian Immigration Centre, which became the head office of Plant Control and Quarantine. Halse was made officer-in-charge of the Division and all import and export work, permits etc, were done from there. The Timber Control office and sugar cane cutting, fumigation facilities were all that remained at the station.

On 1st December 1956 Miss Dohse left Durban for Pretoria and Miss Johnson assumed control. In April of that year Mrs A. Wessels was employed as a clerical assistant and she continued in this post after remarrying and becoming Mrs Breytenbach until July 1975. For a number of years the herbarium was now able to employ students during their vacations and among them was R. A. Lubke who is now lecturer and curator of the herbarium at Rhodes University and W. J. Lawson who contributed over 350 specimens to the herbarium. In May 1956 Mrs M. Carr was employed as a technical assistant in the herbarium. She was one of the longest standing members of staff to fill the post leaving only in November 1962.

During 1957 and the following years it appears the station had a number of burglaries and eventually in 1960 a night watchman and day guard for public holidays and weekends had to be employed to control this. 1958 saw the renaming of the Department to Agricultural Technical Services and Miss Johnson writes in 1959 that the 24th February was 'a great day for the herbarium as strip lighting had been installed. Specimens had to be carried to the windows to see them before'. Extensive repairs and renovations were done to the buildings and all the library books had been dipped in Drexolon against bookworm.

In April R. H. Halse retired from control services and was later employed at Mt Edgecombe. Mr D. Thomas, an entomologist specializing in forest and timber insects was transferred to the station in October 1959. It was the first time an entomologist had been based here since the late 1920's and the office answered many queries from the public. In 1960 Marincowitz left the station and Timber Control was moved to what is now the police station in Gardener Street. He later became head of Plant Control and Quarantine.

In June 1960 the herbarium identified seeds of the water hyacinth, *Eichornia crassipes* , in a court case. Plants were being sold by street-hawkers to up-country customers, who were shown flowering specimens and then given barren plants on the pretext that they had different coloured flowers.

BOTANICAL RESEARCH INSTITUTE

Although most research activities, including entomology and plant pathology, were retained on a regional basis, the planning and co-ordination of research was strengthened by the formation of a number of national research institutes. The Division of Botany became the Botanical Research Institute and the outstations, including the one at Durban were henceforth referred to as Botanical Research Units. The Plant Protection Research Institute was formed to deal with research of a national nature in fields of entomology and plant pathology, which resulted in taxonomic mycology (and the mycological herbarium), previously the function of the National Herbarium, being placed under Plant Protection. Plant Control and Quarantine was also regarded as a national service and became known as the Division of Plant and Seed Control.

On the 2nd April 1962, Mr R. G. Strey was transferred to Natal Herbarium from Pretoria and this led to major new collections being included in the herbarium. The library was re-organized in this year and fans installed in the herbarium roof.

1963 saw Dr L. E. Codd taking over as Director of the Botanical Research Institute and on 31st August Miss Johnson resigned with Mr Strey now becoming officer-in-charge of the unit. A re-organization of the herbarium ensued with five new metal cupboards being added as the collection had grown to 49 717 with the inclusion of Medley Wood's tropical African specimens and large collections of C. J. Ward, K. D. Huntley and D. J. B. Killick. Major improvements were started in the garden and a systematic planting of rare indigenous trees and shrubs began which today represent a unique collection. A photograph was obtained from the Natal Mercury of the occasion when the herbarium was transferred to the Union Government while Medley Wood was still Director, on 30th October 1913. This hangs in the hallway of Medley Wood's house today, together with a number of other photographs.

In November 1963 connections with Entomology were finally severed when Thomas was transferred to Cedara and the cyanide fumigation chamber in which sugar-cane cuttings had still been fumigated by Plant and Seed Control was closed down. A technical assistant post was made available and Miss R. A. Briggs, later to become Mrs Forssman, was sent from Pretoria to fill it.

1964 saw a re-organization of the museum collection, with Medley Wood's material for the technological museum, his fibre and dyed wool samples, Dr Schweickerdt's seed collection, samples of indigenous and imported wood tablets and many other interesting articles being displayed in the entomology building. Strey continued to build this up with his own seed, wood and insect collections and he took considerable interest in gathering information on the early curators of the Botanic Gardens and herbarium as well as early botanical collectors in Natal.

In 1965 Dr Wager retired and an officer of the Natal Region, Mr Levey was stationed at the office with the intention of making the station an extension centre for the Region. In April Wager was employed again as extension officer, but it was decided shortly afterwards to move the office to the newly formed headquarters in Pinetown. Wager, however, remained at the unit until November 1966 before retiring permanently.

HERBARIUM AND BOTANICAL SURVEY

In 1966 it was decided to increase the scope of work at the unit to include taxonomic and ecological research. Botanical Survey activities previously based at Pietermaritzburg were transferred to Natal Herbarium and the herbarium and library expanded. The double garage was built and the government vehicle which had been based in Pietermaritzburg came down to the unit. In January 1967 E. J. Moll, Botanical Survey Officer, was transferred and placed as officer-in-charge of the unit taking over the entomology building as an office. He undertook vegetation studies in Tongaland and completed a project on the three-rivers catchment area south of the Tugela.

The herbarium received 12 new cabinets and the library many additional books, while in March a contractor completed the new tarred road and fence in front of the unit. J. W. Morris, another survey officer, remained in Pietermaritzburg but used the unit as a base until September 1967. In August J. H. Ross of the Flora Section in Pretoria joined the Natal Herbarium to undertake a revision of *Acacia* for *Flora of Southern Africa* and to revise Bews's *Flora of Natal.* In March of the following year, Ross left Botany to help out in the family business but returned towards the end of November to carry on with his research.

During 1968 fluorescent lighting was fitted throughout the buildings although it is unfortunate that the pressed steel ceiling in the herbarium was damaged; and the dark-room was fitted out and made functional. Complete repainting followed in 1969 and a new asbestos roof which was specially made to resemble the original corrugated one was fitted onto the herbarium and house. A large amount of timber was replaced and an air-cooling plant installed in the library.

E. J. Moll returned in August from nearly a year spent in Europe. By mid-1968 the herbarium collection had risen to 58 900 with the inclusion of large collections from Ward, Venter, Strey, Nicholson, Hilliard, Huntley, Tinley, Moll, Morris, Vährmeyer and Coleman. Over the previous few years black staff had been introduced to take over pressing and mounting work to enable those in the herbarium to cope with the increased work load.

In May 1971 C. F. Musil was transferred from Pietermaritzburg to work on the ecology and eco-physiology of aquatic plants in Natal and later he was joined by M. D. S. Nel who, until June of the following year, assisted as a technician in water ecology (Fig. 6). J. H. Ross left at the end of May for Kew as liaison botanist for the Institute. Miss B. D. Pascoe and afterwards Miss Gafney, later Mrs Vorwerk, were botanical illustrators as well as technical assitants at this time and the latter completed many of the drawings for Mr Strey's revision of *Cussonia* which was later published.

At the end of April 1972, Strey retired but returned again in July to carry on at the herbarium. Dr Codd retired as Director of the Institute in 1973 to be succeeded by Dr B. de Winter, and at the end of July of the same year Moll left the Botanical

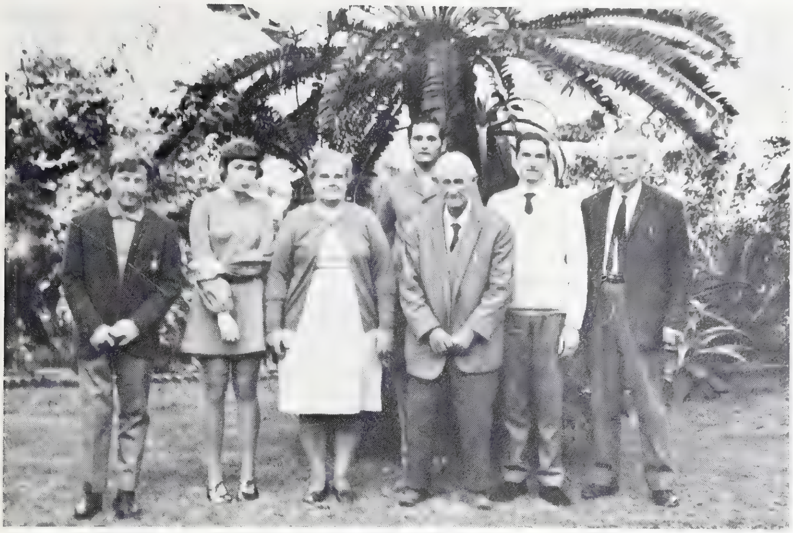

FIG. 6.—Staff of the Botanical Research Unit, Durban, in 1971: Left to right: Mr C. F. Musil, Miss R. E. de Jager, Mrs A. M. C. Breytenbach, Mr E. J. Moll, Mr A. Murray, Dr J. H. Ross and Mr R. G. Strey.

Research Unit to take up a post as lecturer in Plant Ecology at the University of Cape Town. At the same time T. H. Arnold who had recently been employed in Pretoria was temporarily seconded to Natal Herbarium to relieve Mr Strey who intended going overseas on vacation. This fell through, however, and Arnold left at the end of November to complete an M.Sc. at the University of Natal, Pietermaritzburg. Another officer seconded from the Institute. C. H. Stirton, worked on his M.Sc. thesis on *Eriosema,* while employed at the unit from December 1973 to January 1974, but returned to Pietermaritzburg to continue his studies.

At the end of July, 1975, Mr Strey retired permanently and moved to the Village of Happiness near Margate. From his numerous collecting trips, mostly in Natal and Transkei, he contributed well over 6 000 specimens to the herbarium and distributed large quantities of duplicates to all the major herbaria in South Africa. He discovered a new genus and a number of new species some of which he wrote up for publication and his name is commemorated in several of his discoveries. His observations led to the description of *Raphia australis* a new palm species, and the only one of this genus to occur in South Africa. During the period Strey was curator, the overall scientific activity in Natal Herbarium increased as it had not done since the days of Medley Wood.

The Botanical Survey Officer, C. Musil, was in charge of the unit after Strey retired until the arrival of P. C. V. du Toit from Pretoria in April 1976. During this period the museum was arranged and annotated as it is at present. Du Toit was mainly interested in grasses, soon starting work on the genus *Pentaschistis* and his wife, who was also employed at the Institute and transferred with him, worked on illustrations for the Pretoria Flora until 1978 when she resigned. In 1977 the tropical African and extra African collections accumulated by Medley Wood, and the moss collection, were transferred to Pretoria and the herbarium now concentrates on South African flowering plants and ferns with emphasis on Natal. C. Buthelezi, the present black herbarium assistant, joined the staff in 1977.

REGIONAL HERBARIUM

In February 1979 Mrs B. J. Pienaar was employed in a new half-day technician-botanist post and she helped build up the separate cultivated plant section of the herbarium to cope with the increasing demand for identification of exotics. At the end of February, C. Musil was transferred back to Pretoria and this terminated the permanent occupation of the Botanical Survey section at the unit. It is now visited only occasionally by Dr P. J. Weisser, who is surveying the Zululand coastal dunes to establish conservation priorities as the result of dune mining. The new fence surrounding the property was completed in 1980 and in June Du Toit resigned from the Institute and left for Cedara Agricultural College to lecture in pasture management.

On 1st August 1979 B. D. Schrire was transferred from Pretoria as officer-in-charge five months after joining the Institute. The first priority was to establish a mini-herbarium or quick-guide of representative specimens of the Flora of Natal, and close contact with the Institute in Pretoria resulted in the inclusion of many recent revisions and name changes, generally updating the collection to facilitate identification. With the help of Mr G. Nichols of Durban Corporation, the garden has been extensively pruned and cleared of superfluous vegetation while being improved with the addition of many more Natal plants. Mrs Pienaar was transferred to Pretoria in May 1981 being replaced in June by Mrs M. Jordaan (née Prins) a previous employee of the Institute and, together with an additional half-day technician post created in May 1982 to replace the technical assistant post, the herbarium is now able to offer a more effective information and identification service to the public. The collection now stands at over 75 000 specimens mostly representative of Natal. Research is being done into the tribe Desmodieae of the Leguminosae for the *Flora of Southern Africa* and requests for seed or other plant material and general collecting for the herbarium continue as facets of the work done at Natal herbarium today.

This account of the history of Natal Herbarium draws attention to the large contribution made by its staff over the years to agriculture in South Africa and botany in particular. It is fitting, therefore, that the Natal Herbarium is shortly to be declared a National Monument.

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UITTREKSEL

Die geskiedenis van die Natalse Herbarium word beskryf vanaf die beginjare in 1882 tot 1982, die jaar van sy honderdjarige bestaan. Sy geskiedenis is onlosmaaklik verweef met dié van die Durbanse Botaniese Tuin, wat begin het as 'n Landbou-tuin in 1848, en die Durbanse Botaniese Stasie. Die rolle gespeel deur die verskeie kuratore en beamptes-in-beheer, veral John Medley Wood wat 32 jaar lank die pos beklee en veel gedoen het om die Herbarium op die botaniese kaart geplaas te kry, word beklemtoon.

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An African knowledge of ethnosystematics and its application to traditional medicine, with particular reference to the medicinal use of the fungus *Engleromyces goetzei*

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ABSTRACT

Botany and medicine have been closely related fields of knowledge throughout the history of man's development. Consequently a folk knowledge of botanical classification (ethnosystematics) is often rooted in traditional medicine.

Four factors have contributed to ethnosystematics being particularly well developed in Africa. They are: the continuing importance of traditional medicine; the importance of the spoken word in handing down traditional botanical and medical knowledge; the richness and diversity of the African flora; and the many different languages and dialects used by the African people.

Some of the plants used in African traditional medicine are being investigated as sources of antibiotics and other useful substances. An example is the investigation of the fungus *Engleromyces goetzei* P. Hennings, whose medical use is described for the first time.

INTRODUCTION

Gradually, through trial and error, primitive man learned the uses of plants, especially those that served as food and as remedies for disease. To be lasting, this kind of classification of plants required the existence of names, and the practice of giving names to useful plants marked the beginning of systematic botany. This ability to know the names of plants and to identify them in their natural habitats is what I refer to as 'ethnosystematics' i.e. a folk knowledge of botanical classification.

There are several reasons why ethnosystematics is particularly well developed in Africa. Firstly, Africa has a very rich and diverse flora, which has served her people for many thousands of years. Plants are by far the most widely used sources of medicaments in the traditional medicine of Africa. In this traditional medicine man is regarded not simply as an organism on his own, but his sociological environment is also taken into account. Africans have long associated plants with ritual, symbolism and religious beliefs. More ritual symbols are drawn from the plant Kingdom (particularly trees) than from any other part of the environment.

A second reason for ethnosystematics to be well developed in Africa is that the continent is particularly rich in languages and dialects and every ethnic group has names for the plants growing in its environment. In many cases knowledge of plants (and their names) is shared by neighbouring cultures. This is probably because some of the people who make the greatest use of herbal remedies are pastoral tribesmen, who come in contact with other ethnic groups whilst travelling great distances in search of grazing for their livestock.

A good knowledge of ethnosystematics has survived in Africa largely because traditional medicine is still widely practised. In most African countries the majority of people usually live in rural areas where some of the common problems are: lack of communication (transport and telephone) services, low income, and lack of modern medical facilities. The nearest hospital or dispensary may be many kilometres away, and out of reach. Even if he can reach a hospital, the sick person may prefer traditional medicine. Well established traditional practitioners usually have many customers in rural areas — and they all have to be able to identify and know their plants.

The last factor in the survival of a well-developed ethnosystematics in Africa is 'the oral tradition,' which results in knowledge being widely held in the community. Knowledge of traditional medicines is handed down orally by medicine men/women, parents, elders or priests. This involves naming the plants to be used and the diseases to be treated, and observing the preparation and application of the medicaments. This tradition of relaying medical information orally is found in all African countries. Even Ethiopia, which has had its own written language for over 2 000 years, has no written record of traditional medicine.

This oral tradition has all the advantages of a living culture, being continually enriched and reflecting attitudes, beliefs and style of life.

It also has drawbacks. Some of the knowledge is liable to be distorted or lost completely during transfer, therefore becoming both erroneous and dangerous to the recipient. In the absence of an African pharmacopoeia, there is a need to place our knowledge of African traditional medicine and the ethnosystematics on which it relies, on a firmer basis.

TRADITIONAL PRACTITIONERS

The traditional medicine men and women have continued to occupy an important position in our societies. Probably at this stage, we should try to classify them and know who they are. They are

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sometimes referred to as traditional practitioners, healers, witch-doctors and so on. According to their practice, we can group them as follows:

—herbalists who use plants for treating their patients;
—divines (diviners) who are also herbalists but use divinatory procedures for treatment;
—spiritualists who hardly use plants at all for treatment;
—great therapists (also spiritualists) who have power of incantation (charm, magic, spell or formula) and rites.

It is the diviners, spiritualists and the great therapist spiritualists who normally perform ritual ceremonies and prepare ritual medicines to protect people from 'unnaturally' caused diseases, curses or sorcery. What is interesting here is that there is no cure in the world, including western medicine, for a person who has been cursed or bewitched — except via his own traditional beliefs. The victims of mystical misfortunes caused by the sorcery of an enemy or curse of a family member (living or dead) can be treated only by those I call 'advanced' traditional practitioners. A ritual diviner or spiritualist will determine, usually by divination with animal shells or marbles, whether the man has actually been cursed or bewitched, and if so, treat him with magical medicine. The treatment here involves primarily a ritual purification, removal of the original curse or sorcery, and thus removing the physical symptoms as well.

Traditional medicine as practised in Africa, embraces a wide field of medicine and pharmacology including pharmacognosy. These distinct professions as recognized in modern medicine, are usually combined by a single traditional practitioner. A good herbalist must have an excellent memory in order to carry all this information in his head. A traditional practitioner generally provides health care by using plant, animal and/or mineral substances as tangible objects for treating his/her patients. Of the three kingdoms mentioned, plants are by far the most widely used in African traditional medicine. I have observed that in fields of traditional paediatrics, obstetrics and gynaecology, women are excellent and authentic herbalists. Women are also much more liberal in passing on their herbal knowledge to their daughters than men. A man will normally wait until he is old, before choosing one of his sons (usually the first born) and teaching him his medical art. Although the medicine man is usually the more prominent and more popular in our society, the woman was the first physician, probably because of her close association with children who need the most medical attention in a family. One finds that, whereas there may be many practitioners here and there who have mastered small lists of herbal remedies, only a few attain eminence. It must be appreciated that a whole traditional pharmacopoeia known to each practitioner is carried in his/her head, and it includes the recollection of where the plant is to be found as well as the identification of the already prepared decoctions, infusions, ash or other dried leaves, roots and bark stored in the personal pharmacy. The respect the medical practitioner's command among African tribes is reflected by the very eminent names they are referred to in every dialect. And the reputation of 'Bwana Mganga' (Swahili) depends on appreciation of his medicine, therefore, he is usually credited with having 'good medicine' rather than being a 'good doctor'.

THE CONCEPTS OF DISEASES

The concepts of diseases among Africans reflect their culture and can be broadly grouped into two categories. The first group, 'naturally' caused diseases, are those which are due to tangible material which affect the body organs. Such natural diseases are regarded as minor or normal because they can be described by the patient and treated by the doctor in strictly physical terms. It is a common and preconceived belief (fear) that as soon as a disease becomes more acute or severe, it is due to 'unnatural' cause or 'intangible forces' which implies that a hostile person is using supernatural powers against the patient, or that the victim may have transgressed the moral code and incurred the wrath of ancestors. This second group of diseases is generally classified among our people as complicated and serious. Cases are characterized by persistent illness. Bewitched or cursed persons require special types of treatment, medicine and traditional doctors. It is due to such complicated cases that traditional treatment does not only make use of material substances like herbs, but sometimes includes resources drawn from the 'immaterial world.' Perhaps we should at this juncture, define Traditional Medicine as 'the sum total of all the knowledge and practices used in diagnosis, prevention and elimination of physical, mental or social imbalance, and relying exclusively on practical experience and observation handed down from generation to generation.' The term 'medicine' as used here, refers not only to herbs or drugs, but also includes a whole range of charms and amulets, spells and incantation.

PREPARATION AND DISPENSING OF DRUGS

The part of a plant used for preparing a drug depends primarily on the structure of the species. For trees and shrubs, it is a common practice to use the bark and/or roots. It is from such usage that East Africans have coined a colloquial Swahili name for herbal medicine 'miti shamba' meaning 'medicine from the tree.' With small plants and herbs the tendency is to use the whole plant and (by contrast with trees) the leaves are also frequently used. Traditional pharmacognosy is limited in that an extract from one plant is usually dispensed alone. Only occasionally is an infusion with extracts from two or more plant species given to a patient. The methods of preparing plants drugs by African healers are uniform, and are usually accomplished by one or two of the following procedures.

1. *Boiling:* is a common method, especially with roots and bark of trees or shrubs. The decoction is then taken orally or used for

bathing, depending on the nature of the disease.

2. *Soaking in cold water:* is generally used with crushed leaves or small herbaceous plants, and the concoction used as in the first method.
3. *Burning:* is also used with leaves and small herbs after the material has been dried. The ash can be licked, rubbed directly onto the wound, soaked in water and drunk or gargled in the mouth.
4. *Chewing:* is a first aid method of preparing a drug, especially for treatment of snake-bite, stomach disorders or for mouth and throat ailments.
5. *Heating or roasting:* is usually for preparing succulent leaves or other plant parts as a poultice (a kind of moist dressing applied on an inflamed part).
6. *Crushing or pounding:* normally precedes other methods such as boiling, soaking or burning. Crushed material may alternatively be applied directly onto a wound, usually after being mixed with some kind of oil.

What is interesting about all the six methods of preparing herbal remedies is that each of them attempts to extract whatever active principle is contained in the plant before it is dispensed to the patient. To the herbalists, the preparation is done in order to obtain the 'power force' of the drug. Practically all herbalists have some kind of pharmacy with ready made decoctions, infusions, instillations, powdery ash, inhalations, plasters, fomentations, enemas, embrocations, fumigations and bandages (usually made from dry pseudostem portions of banana). Another common feature of leading herbalists is the tendency to own a private garden where they grow special medicinal plants. In such a garden, they normally grow valuable herbs which are not growing naturally within their village. In this way, the supply of fresh drugs is made available to the customers as the demand may arise.

The method of dispensing the drug depends largely on the type of disease to be treated. Aromatic drugs for treating influenza or similar diseases are customarily used in steam form. Traditionally, drugs are frequently taken with various types of food stuffs. The pastoral tribes usually take their drugs in milk, others use soup, porridge (especially that made from the African millet flour, *Eleusine coracana*), honey, blood, and various kinds of native beer. It should be noted that the majority of the food stuffs used are in liquid form, and are both nutritious and appetising. Remember that most plant parts used for preparing herbal remedies can be sour, bitter or with offensive smell. Such drugs are usually mixed with a favourite food to make them more palatable.

AFRICAN USE OF HIGHER PLANTS IN TRADITIONAL MEDICINE

The overall number of drug plants used in Africa is so large that it would be unrealistic to try to list them in this paper. Specific examples can be read in the already available literature, e.g. Kokwaro (1976).

Apart from indigenous plants, a number of introduced or naturalized plants have now encroached into traditional medicine. A number of gum trees (*Eucalyptus* species) introduced from Australia usually have their aromatic leaves used for treating influenza. The same usage is employed on Citrus. Pride of India (*Melia azederach*) bark is used in Zaire and West Africa as an anthelmintic. Castor oil plant (*Ricinus communis*) which grows widely all over Africa is widely used as a purgative.

AFRICAN USE OF LOWER PLANTS IN TRADITIONAL MEDICINE

Lower plants are not as frequently used by Africans in their traditional medicine as are higher plants. Africans living in the East African highlands have, however, learnt to use a particular fungus which grows in the montane bamboo forests. This plant, is probably the fungus most widely and successfully used medicinally in East Africa. Its scientific name is *Engleromyces goetzei* P. Hennings. Although I had been studying its use in the Kenyan highlands since 1968, I had insufficient information to include it in my 'Medicinal Plants of East Africa' (1976). This is the first full report on the occurrence and use of the plant.

Engleromyces goetzei

General notes

Engleromyces is a monotypic genus belonging to the family Xylariaceae. It is usually placed in the order Sphaeriales of the Pyrenomycetes, but some authorities prefer to regard it as an ascomycete.

It is a semi-solid structure which can grow to the size of a football and weigh up to 4 kg. The flesh of the interior is like a heavy cake, resembling the local maize-bread 'ugali.'

Its Kikuyu name 'Kieha-kia-Murangi' means 'that which sits on the bamboo' and *Engleromyces goetzei* is in fact a parasite found only on the upper stems of the mountain bamboo *Arudinaria alpina.* It partially envelopes the bamboo stem, often forming two lobes, hence its English name 'baby's bottom' (Figs 1–4). Early specimens sent to European herbaria fascinated botanists, who also likened them to human skulls.

General distribution

Engleromyces goetzei has been reported from the Rungwe Mtns of southern Tanzania, the Ruwenzori Mtns (Uganda and Zaire), Echuya Forest in Kigezi District of Uganda and on the Virunga Mtns of Kivu Province in Zaire. In Kenya it occurs on Mount Kenya and the Nyandarua Mtns (Fig. 5).

Mount Kenya is located on the Equator and is, at 5 195 m, the second highest mountain in Africa.

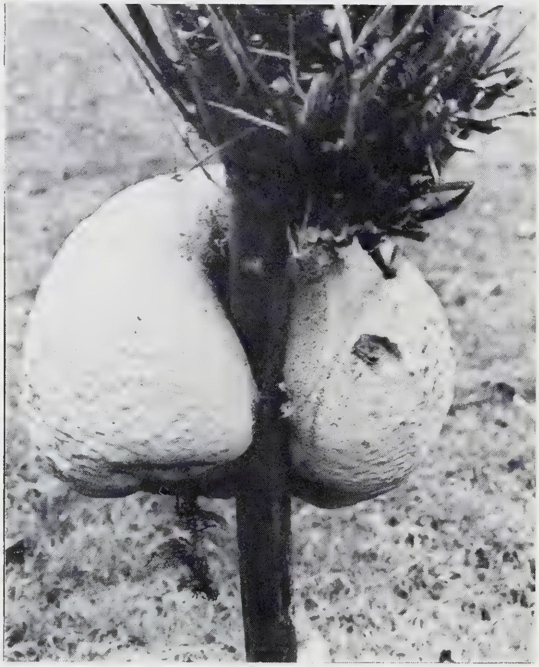

FIG. 1.—*Engleromyces goetzei* growing on a bamboo stem, near Kiondogoro Gate, Nyandarua Mountains, Kenya. Photo: J. O. Kokwaro.

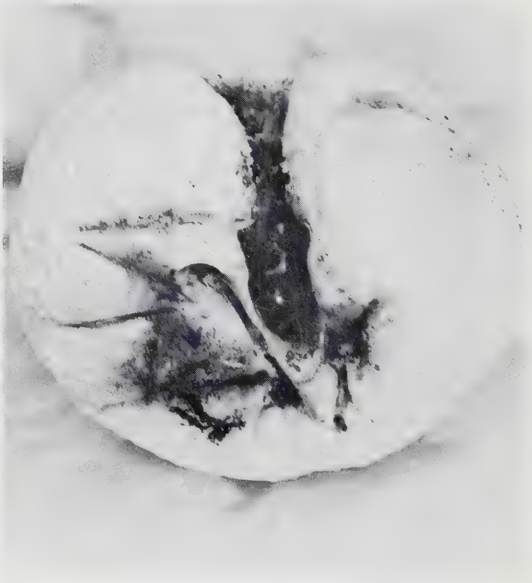

FIG. 2.—Adaxial surface of a mature *Engleromyces goetzei* showing the point of attachment to the bamboo stem. Photo: J. O. Kokwaro.

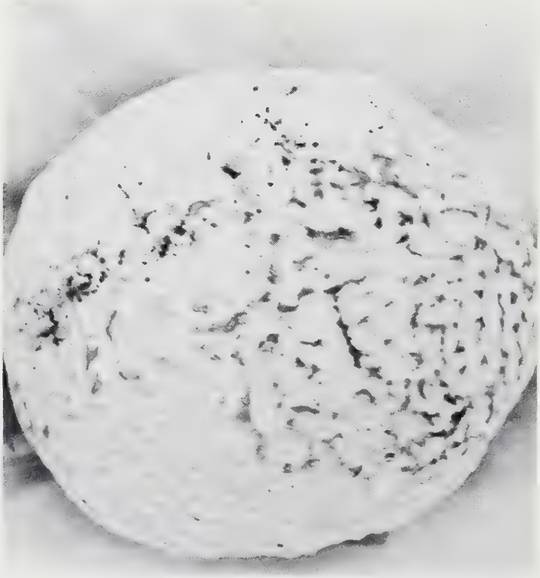

FIG. 3.—Abaxial surface of a mature *Engleromyces goetzei* showing the characteristic foveolate pattern. Photo: J. O. Kokwaro.

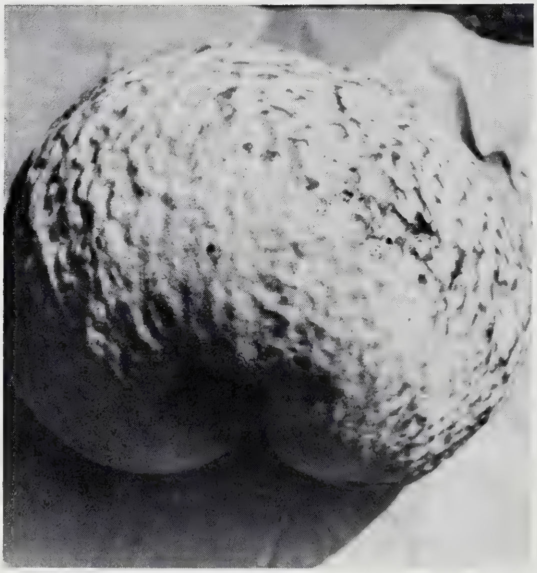

FIG. 4.—The lower part of the photograph shows why *Engleromyces goetzei* was called 'Baby's bottom,' and the horizontal upper surface shows its similarity to a human skull. Photo: J. O. Kokwaro.

The Nyandarua mountains consist of a 100 km long range, running from north to south between the Great Rift Valley and the Laikipia Plateau. Its northernmost summit, Satima (3 000 m) is close to the Equator. Other peaks include Kinangop (3 906 m), the Elephant (3 589 m), and Kipipiri (3 349 m).

Ecology in Kenya

Both Mount Kenya and the Nyandarua Mtns are volcanic and, despite their location on or close to the Equator, both mountains have cold, wet climates. Frost is common on Nyandarua above 2 750 m, and

Mount Kenya has a permanent snow-cap and a number of glaciers. The annual rainfall in the Bamboo zone, where *Engleromyces* occurs, varies from 750 mm to 1 750 mm on Mt Kenya, and from 750 mm to 2 000 mm on Nyandarua. On the western slopes of Nyandarua, the bamboo zone lies between altitudes of 2 700 m and 3 200 m, whereas on the Eastern slopes it is between 2 400 m and 3 000 m. The bamboo zone is very extensive on the Nyandarua Mountains and forms conspicuously distinct stands on Kinangop and Satima peaks at altitudes of 3 100 m to 3 300 m. Bamboo distribution is fairly constant and continuous on the lower zones of both Mt Kenya and the Nyandarua Mtns, except on their northern flanks.

Traditional uses

Although this fungus occurs in other bamboo forests of East Africa and Zaire, its medicinal use has only been reported from Kenya. My professor, Olov Hedberg, first collected *Engleromyces* from Mt Kenya in 1948, and was told by his field assistants that 'it is good against fever.' I was told the same story in 1968 and 1970 (Mt Kenya), 1972 and 1979 (Nyandarua). During and after the emergency periods, from 1952 to 1963, a number of Mau Mau freedom fighters lived in the forests of the two mountains. Since they could not use normal medical facilities, they frequently resorted to traditional medicine for treating their ailments. The climate on the mountains is cold, and some of the frequent diseases there are, pneumonia, colds and fever. The 'baby's bottom' is a reputed medicine among the Kikuyu against these ailments as well as headache (malaria being associated with it), psychosomatic problems, and liver diseases. They have discussed other internal diseases, but it is rather difficult to know exactly what they mean unless they mention a particular organ.

The elderly Kikuyus know the fungus so well that those now living in Nairobi can easily identify it. On 16th June 1979, I collected a sample near Kiandogoro Gate of Nyandarua Mtns. I brought the specimen to the department of Botany at the University of Nairobi, and I was met with remarks such as, 'Ah, you have brought the medicine!', 'May I have a piece of it, please.' In the forest, this fungus is a rare and precious commodity to get. This is obviously because it grows in real thick bamboo forest where there are lots of elephants, and also because it is heavily hunted for by those who know its medicinal value.

Medicinal use of 'baby's bottom' is also recorded from the Mau Range along the western massif through Elgeyo Escarpment to Cherangani Mtns wherever bamboo occurs. It is most likely that the Ndorobo, the original forest dwellers in Kenya, made use of it. The Marakwet know its medicinal value and call it 'Mandewap tegat.'

Treatment

All fevers (flu and colds), pneumonia, headaches, malaria, mental diseases, and thrush are treated by burning the fungus and inhaling the smoke, boiling the fungus and inhaling the steam, chewing fresh material or licking burnt ash. As a purgative, a decoction or infusion is used. It is also used for several systemic diseases including liver diseases and abdominal pains.

Since *Engleromyces* is reputedly effective in curing conditions caused by viruses and bacteria it was thought that it might contain antibiotics active against both groups of organisms. These antibiotics could possibly be similar to Aureomycin (a tetracycline drug which is used in treating penicillin-resistant viruses or bacteria), or erythromycin (another antibiotic group currently used against infections which have become resistant to penicillin). But the 'baby's bottom' is apparently closer in activity to aureomycin than to erythromycin because the latter is active against gram-positive organisms except Heissoria, ± *Haemophilus influenzae* and inactive against gram-negative bacteria. The Kenyan fungus may contain cytochalasins, (recently discovered anti-biotic mould products). The Germans recently discovered antibiotics from *Phoma* species *(Deuteromycetes)*, which they named Phomins, antibiotics with cytostatic activity (preventing the multiplication and growth of cells). Phomins are, however, simply another group of cytochalasins from a different group of fungi.

These deductions have proved well founded, since, from the material supplied by author of this paper to the Department of Chemistry, Odense University in Denmark, a new cytochalasan has been isolated and named *Engleromycin.* It remains for *Engleromycin* to undergo clinical testing.

CONCLUSIONS

It is quite evident that one of the many uses of African flora is in traditional medicine, and from traditional medicine we can discover new compounds which can be used in modern medicine. We are also aware that populations in most African countries are increasing at a more rapid rate than their respective national incomes. Much African natural vegetation has to be cleared to give way for agricultural land to feed the nation. In a number of cases, important medicinal plants are simply harvested from the natural vegetation, but no replanting is done. This poses the problem of extinction of species, particularly trees. African governments are, therefore, encouraged to preserve indigenous forests, include in their botanical gardens a section on medicinal plants, and have seed banks of indigenous economic plants apart from the cultivated crops. There is also an urgent need for chemical, pharmacological and clinical work to be done on the already known African medicinal plants before the knowledge is lost and the plants become extinct.

UITTREKSEL

Plantkunde en medisyne is regdeur die geskiedenis van die ontwikkeling van die mens, vakgebiede wat na aan mekaar verwant is. Vervolgens spruit 'n

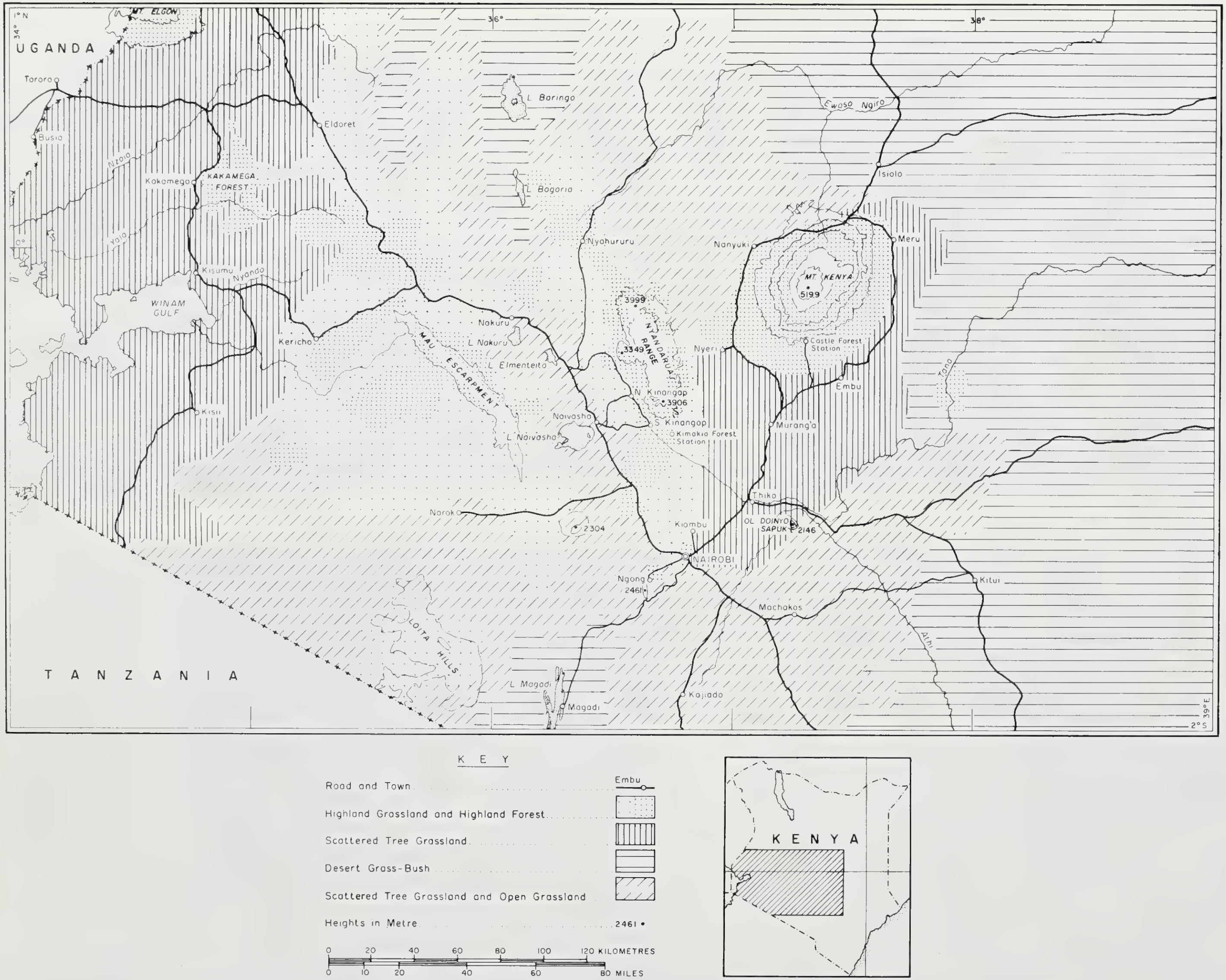

FIG. 5.—Map of Kenya showing main vegetation types. The small map shows the distribution (hatched) of *Engleromyces goetzei*.

volkskennis van botaniese klassifikasie (etnosistematiek), dikwels voort uit tradisionele medisyne.

Vier faktore het bygedra tot die besonder goed ontwikkelde etnosistematiek van Afrika. Dit is: die deurlopende belangrikheid van tradisionele medisyne; die belangrikheid van die gesproke woord by die oorlewering van tradisionele botaniese en mediese kennis; die oorvloed en verskeidenheid van die flora van Afrika en die baie verskillende tale en dialekte gebruik deur die mense van Afrika.

Sommige plante wat gebruik word in die tradisionele medisyne van Afrika word ondersoek as bronne van antibiotika en ander bruikbare stowwe. 'n Voorbeeld hiervan is die navorsing op die fungus Engleromyces goetzei *P. Hennings, waarvan die mediese gebruik vir die eerste keer beskryf word.*

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A study of wood use for fuel and building in an area of Gazankulu

C. A. LIENGME*

ABSTRACT

The utilization of wood for fuel and building timber was studied in a 13 000 ha area of Gazankulu, near Giyani. Headloads of firewood brought in by eight of the 978 families present were monitored during six periods in a year.

The two most important sources of firewood are *Colophospermum mopane* and *Combretum apiculatum*. Firewood consumption is estimated at an average of 14,9 kg per family per day. The annual demand for firewood in the whole study area is, therefore, approximately 5 300 tonnes. Living-huts and storage-huts in the process of being built were examined. The mean volumes of wood in living-huts and typical storage-huts are 1,30 m^3 and 1,09 m^3, respectively. 89 living- and 80 storage-huts were built in a year. The demand for finished timber in the study area in that year was approximately 231 tonnes.

Timber use has not yet outstripped production, but it will do so soon if alternative timber sources are not provided.

1 INTRODUCTION

This study was undertaken because of concern at the deforestation taking place in heavily-populated rural areas of the Transvaal. During a preliminary study of plant uses in Gazankulu (Liengme, 1981) the collecting of firewood and building timber was identified as an important contributor to deforestation in Gazankulu, the Tsonga homeland in the north-eastern Transvaal. The use of wood for these purposes is poorly documented (Liengme, 1983).

The present study was undertaken in 1980 and 1981, in order to provide quantitative data on the demand for wood and on selectivity in wood gathering.

1.1 *Literature review*

Investigations into the use of firewood in rural areas and its consequences, have been undertaken in Zimbabwe (Banks, 1980; Furness 1981(a); Johnston, 1980; Whitlow, 1979) and Malawi (Jackson, 1980; Nkaonja, 1981). Proposals for the solution of the problem, including the establishment of woodlots, proper management of existing resources and increasing the efficiency of use of firewood, have been put forward (Banks, 1981; Fuller, 1980, no date; Furness, 1981(b); Jackson, 1980; Nkaonja, 1981). Species trials of both fast-growing exotics *(Eucalyptus* spp. and *Leucaena leucocephala)* and indigenous species (*Acacia* spp.) have been established in Malawi as part of the Rural Fuelwood Research Project (Jackson, 1980). Woodlots have also been established in Lesotho (Baines, 1980). In Botswana, a study of the firewood situation in south-western Kgatleng has recently been undertaken (Jelenic & Van Vegten, 1981). The establishment of woodlots is proposed to counter the total removal of firewood species from natural communities.

Le Roux (1981, p. 27) sums up the situation with regard to rural firewood use in South Africa as being one of '. . . a vast imbalance between supply and demand.' He estimates that 7,23 million m^3 of firewood are required per annum by the rural populations of South Africa, based on a per capita consumption of 0,6 m^3 per annum.

Although there are extensive areas forested under exotic species (1,158 million ha) in South Africa, the main object of these plantations is the production of sawtimber, pulpwood and poles. The area under woodlots for firewood (excluding woodlots on private farms, the extent of which are unknown) is approximately 18 500 ha. Most of this area (12 000 ha) is in northern Natal. The regions in which the firewood problem is critical are those with a rainfall of less than 500 mm. It is in these regions that little attention has been paid to afforestation and the establishment of woodlots. Trials of woodlot species suited to these regions have yet to be undertaken (Le Roux, 1981).

When the present project was conceived no in-depth study of the use of wood in rural areas in South Africa had been completed. Since then Best (1979) has completed a study of the use of fuels of all kinds, including wood, in three villages; Malefiloane in Lesotho, Jozanna's Nek in the Transkei and Mashunka in the Msinga District of KwaZulu. Annual firewood consumption in these villages was calculated at 1,499, 1,705 and 4,824 tonnes per family respectively. The high value for the last village, relative to the other two, reflects the greater availability of firewood in the vicinity of that village.

A second project, a study of wood use and its effects on the environment, is being undertaken in the Mahlabatini District of KwaZulu (Gandar, 1981). The consumption of firewood in a lowland situation in the area is estimated at 21,1 kg per family per day, equivalent to 7,7 tonnes per family per annum. In upland situations, where wood is scarce, consumption is 33% lower.

There is little documented quantitative data on the use of timber for building. Knuffel (1973) studied in detail the construction of a bee-hive grass hut by the amaNgwane of the Upper Tugela Reserve in Natal. He noted that 228 laths and 26 poles were used, but did not estimate their volume. Gandar

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(1981) is investigating the use of wood for building in the Mahlabatini District. He found large differences in the amounts of wood used in upland and lowland situations. The volume of wood in structures standing at any one time was found to be 3,08 m^3 per family for huts and 3,30 m^3 for stores and kraals in lowland situations as opposed to 1,60 m^3 and 1,37 m^3 respectively, in upland situations.

1.2 *The study area*

An area just to the south-east of Giyani was chosen for study (Fig. 1). The area is well-wooded, ensuring that the people are not limited in the amounts of wood they can gather. There is also a wide variety of woody species present (Appendix 1), giving the opportunity for selectivity in wood-gathering.

The study area consists of three settlements, Ka-Homu A and B, and Ka-Mapayeni (Fig. 2). These settlements form a unit, sharing much of the surrounding woodland as a wood resource area. The total area of land allocated to the three settlements is approximately 18 000 ha, of which approximately 5 000 is residential and cultivated land. The actual population of the area is in doubt, but in 1980 there were 978 families living there (Gazankulu Department of Agriculture and Forestry, 1981).

The people are basically subsistence agriculturalists and depend almost entirely on the local vegetation for fuel and building timber. Even in the nearby town of Giyani, where electricity and other forms of energy are available, wood is still used as a fuel by some people. The sale of wood in the town provides some inhabitants of the settlements in the study area with income. (The rate at which the town is supplied with wood from the study area was not investigated during this project.)

According to Acocks (1970), the study area falls across the boundary between Arid Lowveld (veld type 11) and Mopane Veld (veld type 14). A detailed survey of the vegetation in Gazankulu (Loxton, Hunting Assoc., 1972) shows the vegetation of the study area to consist of a mosaic of woodland communities, dominated by *Colophospermum mopane, Combretum apiculatum* and *Combretum collinum* subsp. *suluense,* together with narrow strips of thicket and tall forest fringing the rivers.

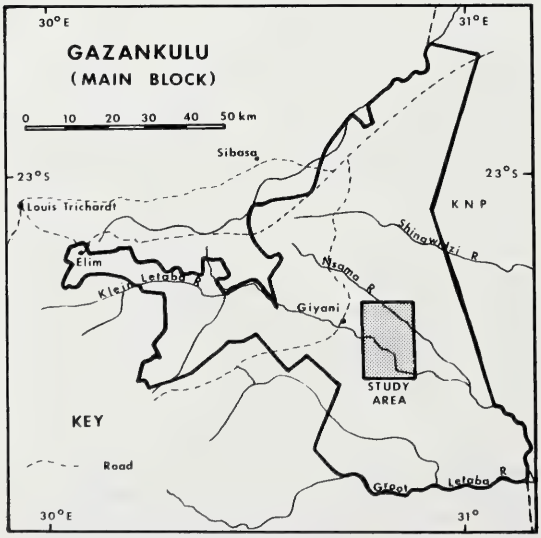

FIG. 1.— Map of Gazankulu, showing the location of the study area.

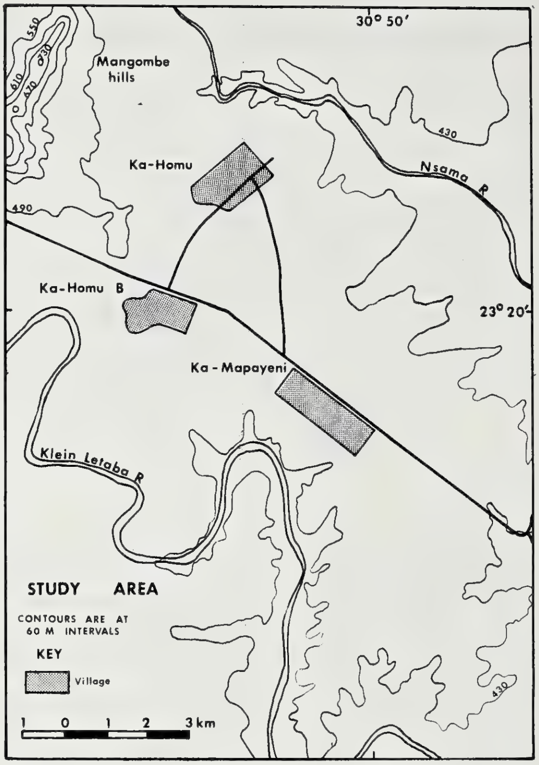

FIG. 2.— Map of the study area.

2 METHOD

2.1 *Firewood*

Initially nine families were interviewed; three in each of the villages Ka-Homu A (village 1), Ka-Homu B (village 2) and Ka-Mapayeni (village 3). Information on the following aspects of firewood use was obtained:

family size
number of fires made per day
preferred firewood species
collecting of live or dead wood
place of collecting
frequency of collecting
time spent collecting.

The firewood collecting of these families was monitored at six periods during a year, in June, August, October and November/December 1980 and February and April 1981. During this time the number of families monitored was reduced to eight, since one family either was absent or had brought in cart-loads of wood prior to the monitoring period and were not collecting.

The operative factor limiting the number of families monitored was the number of headloads that could be analysed in one day, should all women of all families collect on the same day.

The time spent studying firewood in each period was not constant. When productive, 12–14 days were spent in the field on each visit, but during the last three visits monitoring was cut to 7 days. The reason for this was that the women were busy ploughing, cultivating and harvesting at these times. Rain also made it difficult to get to the families.

Analysis of the headloads involved:

1. weighing the entire headload, to the nearest 200 g, on a 50 kg spring scale
2. separating the wood in each headload into the various species (familiarity with the wood was achieved by making a reference collection of the woody species of the area prior to starting the project)
3. weighing the wood of each species
4. counting the number of pieces of wood in each of 5 diameter size classes (< 2,5 cm; 2,5–4,9 cm; 5,0–7,4 cm; 7,5–9,9 cm; > 10 cm).

The women were asked how long each headload would last them and any interesting aspects of collecting were noted.

From the above data the following were calculated:

1. mean daily consumption of firewood per family, for each period and overall (firewood consumption was calculated on a family basis rather than on an individual basis because the family is the functional unit consuming the wood)
2. mean headload weight
3. the relative proportions of woody species occurring in headloads, calculated both on a percentage weight basis and a percentage frequency of occurrence basis
4. the diameter size class distribution of pieces of firewood, for each species and overall.

2.2 *Building timber*

The use of timber for building was studied during two winter seasons in 1980 and 1981. It is at this time of the year that most of the building is done. Living-huts and storage-huts (granaries) are the major structures built, fences and cattle stockades contributing only little to the total number of structures erected in one year. These latter two structures are irregular in size and shape, being sometimes solid wooden structures and other times pole and barbed wire structures. For these reasons, it was decided not to include cattle stockades and fences in the study.

The living-huts and storage-huts were examined when the wooden framework of the structure was completed, prior to mud-plastering, bricking-in or thatching.

2.2.1. *Living-huts*

Twenty living-huts were examined. The wooden framework of a living-hut (Fig. 3) comprises the following: (a) wall poles; (b) roof poles; and (c) withes (which are laid across the roof poles and along the top of the wall). The length and average circumference of each pole in the wall were measured (to the nearest centimetre and 0,5 cm, respectively). One quarter of the roof was randomly selected and the length and average circumference of each roof pole in that quarter measured. The length of withes used in a quarter was also measured and a mean withe circumference was calculated from a sample of 20 measured circumferences.

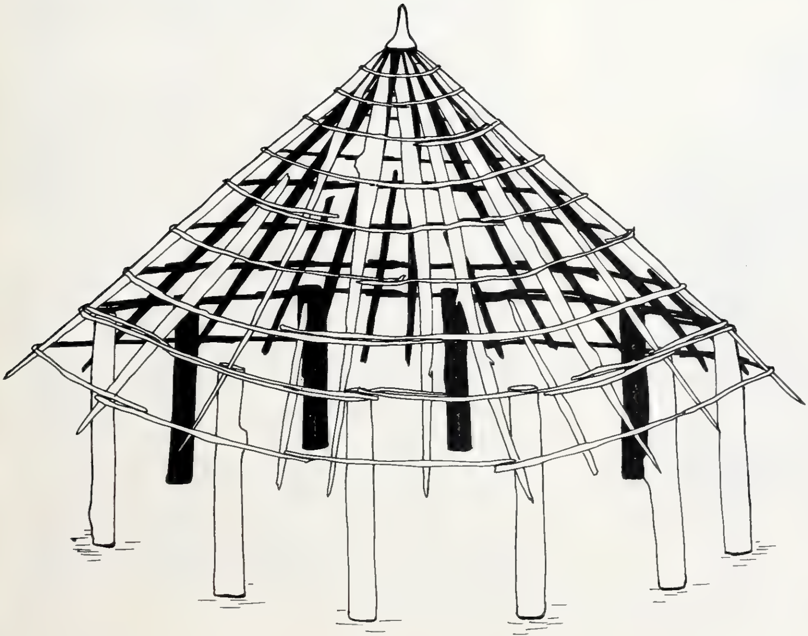

FIG. 3.— The wooden components of a typical round living-hut.

The volume of wood used to build each living-hut was calculated from these measurements, using the following formulae:

$$\text{volume} = (\text{circumference})^2 \times \text{length}$$

total volume = (Σ volumes of the wall poles)
+ [(volumes of the roof poles measured)
+ (Σ volumes of the withes measured)] × 4

Each piece of wood was identified to species.

2.2.2 *Storage-huts*

15 storage-huts were studied in the same way as the living-huts. A storage-hut consists of the following wooden components: (a) a raised floor, supported on two or three large poles, which are in turn supported on short Y-shaped stumps; (b) a wall made of large and small poles; (c) roof poles; and (d) withes, around the wall (inside and outside) and across the roof poles (Fig. 4).

The floor proved difficult to measure, since there was often maize stored inside the hut and getting in under the floor was sometimes impossible, because it was usually only 30–50 cm off the ground. Therefore, the end circumferences of the floor poles were measured rather than the average circumferences.

One quarter of each storage-hut was selected (again randomly) and the wood used in the wall and roof measured as described for the living-huts. The volume of wood in each storage-hut was calculated as below:

$$\text{volume} = \frac{(\text{circumference})^2}{4} \times \text{length}$$

total volume = [(Σ volumes of the wall poles measured)
+ (Σ volumes of the roof poles measured)
+ (Σ volumes of the withes measured)] × 4
+ (Σ volumes of the floor poles).

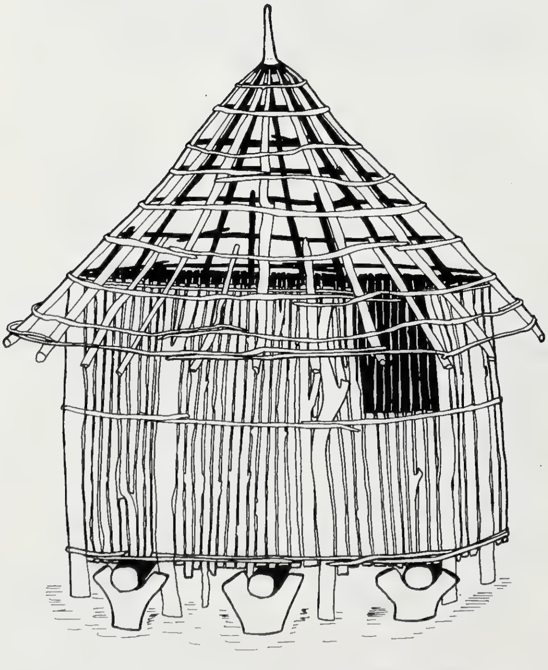

FIG. 4.— The wooden components of a typical storage-hut.

2.2.3 *Statistics on building*

Statistics on the numbers of permits, to cut wood for building, sold in the study area, were obtained from records at the Giyani magistrate's offices. For every structure built, a fee has to be paid and a permit obtained. These permits are sold by the tribal authority for the area, whose local representative is the chief under whom the three study villages fall. Since the people still respect the chief's authority and also because there is a fine for illegally cutting timber, the statistics are assumed to reflect reasonably accurately the actual number of structures built.

2.3 *Overall wood use*

The overall weight of wood used for firewood and building per annum in the study area was estimated, as follows. The total weight of firewood used in a year by the population of the study area was calculated, as was the total volume of building timber cut for living-huts and storage-huts in a year. Timber was converted to approximate weight (air-dried) using wood density data (Van Vuuren, *et al.* 1978).

3 RESULTS

3.1 *Firewood*

3.1.1 *Background information*

The average size of the families whose firewood collecting was monitored was 7,1 persons. This does not include men working away, who are absent most of the year. It is also not a true reflection of real family size since, in some cases, what was taken as a family unit for the purpose of the survey, was an extended family group. The criterion for considering such a group as a single unit was whether or not cooking was usually done on a single fire, in which case if more than one woman collected firewood, this resource was pooled.

All the women interviewed agreed that *Colophospermum mopane* and *Combretum apiculatum* are the best species for firewood. Neither species was given as the single best firewood species; both names were always given in reply to the question. The reason given for this choice was that the wood of these two species produces good coals. Other species also mentioned as producing good firewood were *Combretum imberbe* and *Acacia nigrescens.*

The women said they collected only dead wood — either fallen or standing. It was later found that a little wet wood was collected, that had been cut in the clearing of fields.

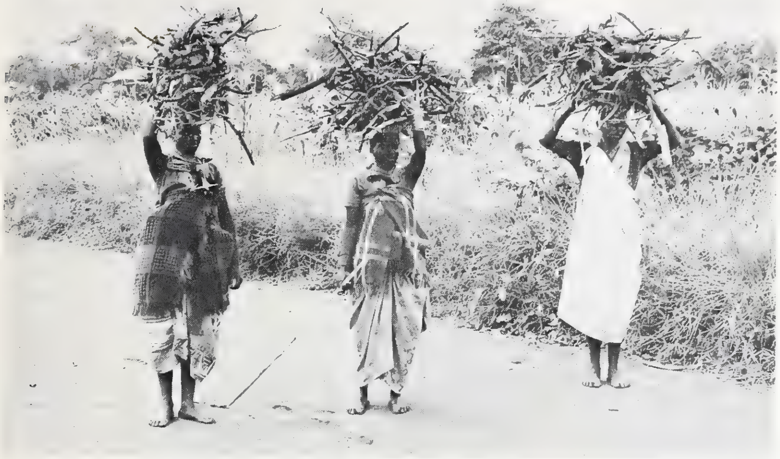

FIG. 5.— Women returning from firewood gathering.

One of the families sometimes made use of a 'scotch-cart' for collecting wood; the collector then spent most of the day out collecting. This family also sold wood in the town, Giyani, at R10,00 a load.

Of the remaining seven families only two said they collected relatively near the village. There is, however, little dead wood remaining in the vegetation near the villages and the women of the other five families collected wood as far afield as 4–5 km from home.

Generally, a group of several women goes out collecting together, leaving early in the morning and returning three to six hours later. Firewood is collected three or four times a week in winter and twice a week in spring and summer. Wood is often stockpiled in preparation for the cultivating season since, once that has started, there is little time for collecting firewood, except in small quantities.

Three cooking fires are usually made each day. In winter, cooking fires may be kept going for warmth, especially at night and in the early morning. Fires, specially for warmth, are also made.

3.1.2 *Consumption of firewood*

The overall mean consumption of firewood for the eight families was 14,9 kg per family per day. In terms of annual consumption this represents 5 438,5 kg or 5,4 tonnes per family.

Table 1 gives the weight of firewood used per day by each family during each of the six monitoring periods. Several gaps appear in the table, due to a number of factors. Firstly, the women of families 2, 5 and 7 were harvesting crops throughout period 6, only collecting wood as they walked home in the evenings. This was used up by the following morning. Secondly, the entire family 5 was absent during period 5. Thirdly, the women of family 6 started working in Giyani half-way through the project and despite repeated visits during weekends, no data were obtained for periods 4, 5 and 6.

3.1.3 *Seasonal variation in consumption*

It can be seen from Table 1 that firewood consumption was very variable from one family to another and from one monitoring period to another. There was, however, a general trend to approximately 40 higher consumption in period 2 (August) than at any other time.

3.1.4 *Average weight of headloads*

The mean weight of all the headloads examined (191 headloads) was 29,95 kg (Table 2). The mean weights of headloads in the different families varied from 15,77 kg to 39,31 kg.

TABLE 1. — Firewood consumption (kg per family per day)

	Family								
Period	1	2	3	4	5	6	7	8	Average
1	22,1	10,0	16,4	14,6	15,9	26,0	9,3	9,9	15,7
2	31,8	28,0	13,3	29,4	18,5	18,8	11,8	14,3	21,6
3	15,5	15,6	12,9	11,2	13,9	6,5	8,6	11,1	12,1
4	17,7	17,5	7,7	10,0	12,1	—	9,0	16,7	13,0
5	9,8	14,6	9,5	15,0	—	—	9,4	14,7	11,8
6	13,6	—	9,9	9,1	—	—	—	11,1	11,4
Overall	21,9	17,4	11,8	18,4	15,1	16,6	10,7	12,3	14,9

TABLE 2. — Mean weight of headloads (kg)

Family	Mean weight of headloads
1	37,28 ± 11,06
2	39,31 ± 12,30
3	15,77 ± 12,71
4	30,00 ± 8,87
5	36,74 ± 9,59
6	24,39 ± 8,53
7	23,38 ± 9,49
8	27,38 ± 7,95
Overall	29,95 ± 12,44
Excl. Fam. 3	31,64 ± 11,39

A second overall mean headload weight was calculated excluding the loads collected by family 3. This family sometimes collected by cart, but when headloads were collected, it was young girls who did the collecting and their bundles were consistently small. This second mean was 31,64 kg.

The heaviest headload weighed was 67,2 kg. Fig. 6 shows the distribution of headloads in weight classes.

3.1.5 *Species used as firewood*

Altogether, 42 species were found to be used as firewood. These are listed in Appendix 2. The three most commonly collected species, *Colophospermum mopane, Combretum apiculatum* and *Acacia nigrescens,* made up 77,2% by weight of the wood. Table 3 shows the eight most commonly collected firewood species, accounting for over 90% of the wood gathered. The remaining 34 species accounted for only 7,6% of the weight of wood collected. Their contribution is of marginal importance and their collecting is perhaps incidental to the main task.

Of the species most commonly collected by each family, *C. mopane* is the most common in five cases, *C. apiculatum* in two cases and *A. nigrescens* in one case.

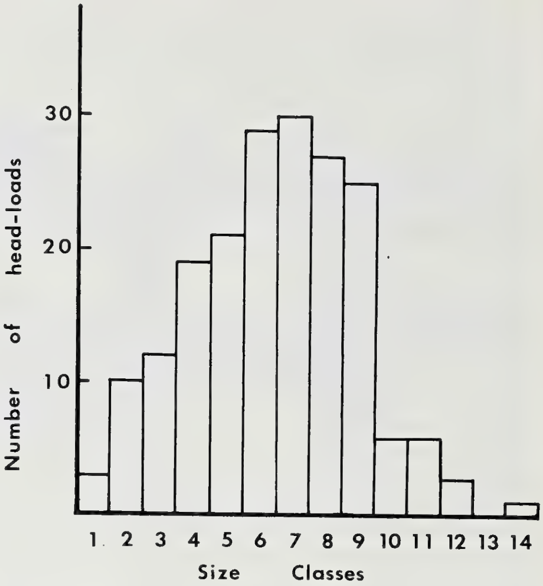

FIG. 6.— The weight-class distribution of the headloads weighed. Weight classes are: 1, < 5,0 kg; 2, 5,2–10,0 kg; 3, 10,2–15,0 kg; 4, 15,2–20,0 kg; 5, 20,2–25,0 kg; 6, 25,2–30,0 kg; 7, 30,2–35,0 kg; 8, 35,2–40,0 kg; 9, 40,2–45,0 kg; 10, 45,2–50,0 kg; 11, 50,2–55,0 kg; 12, 55,2–60,0 kg; 13, 60,2–65,0 kg; 14, > 65,0 kg.

Analysis of the firewood species on the basis of the frequency of occurrence in headloads (Table 4) shows the same eight species as being the most frequently collected.

3.1.6 *Size of wood (diameter)*

More than 80% of the pieces of wood collected were less than 5 cm in diameter (Table 5) and more than 50% had a diameter of less than 2,5 cm. The length of pieces was not recorded.

TABLE 3. — Major woody species collected as firewood and their proportionate weights

Species	Family								Overall
	1	2	3	4	5	6	7	8	
Colophospermum mopane	22,9	57,9	7,6	38,5	16,5	52,3	60,8	54,1	38,7
Combretum apiculatum subsp. apiculatum	27,4	6,1	40,6	25,6	65,6	13,2	15,9	3,7	23,0
Acacia nigrescens	31,1	21,0	5,1	15,6	3,8	9,2	12,0	4,4	15,5
Pterocarpus rotundifolius subsp. rotundifolius	0,5	7,8	—	12,2	8,6	0,2	0,3	5,4	4,6
Combretum collinum subsp. suluense	1,4	1,5	3,3	2,7	3,3	5,7	1,1	14,6	3,8
Combretum imberbe	0,2	0,8	11,2	0,1	—	10,7	3,2	1,3	2,6
Sclerocarya birrea subsp. caffra	3,1	0,1	3,1	1,7	—	0,5	0,1	9,9	2,4
Combretum hereroense	—	1,7	5,1	—	—	4,2	2,8	2,2	1,7
Others**	13,4	3,1	24,0	3,6	2,2	4,0	3,8	4,4	7,6

**See Appendix 2.

TABLE 4. — The percentage frequency of occurrence* of the 8 major firewood species collected

Species	Family 1	2	3	4	5	6	7	8	Overall
Colophospermum mopane	45,1	85,7	40,0	81,5	85,7	89,5	87,0	88,0	74,6
Combretum apiculatum subsp. apiculatum	57,6	25,0	65,0	70,4	100,0	52,6	60,9	28,0	54,4
Acacia nigrescens	48,5	42,9	25,0	37,0	7,1	52,6	39,1	12,0	34,2
Pterocarpus rotundifolius subsp. rotundifolius	15,1	25,0	—	29,6	42,9	15,8	4,3	16,0	18,1
Combretum collinum subsp. suluense	24,2	21,4	35,0	29,6	42,9	57,9	21,7	48,0	32,6
Combretum imberbe	6,1	7,1	35,0	3,7	—	42,1	30,4	8,0	15,0
Sclerocarya birrea subsp. caffra	18,2	3,6	15,0	11,1	—	5,3	4,3	24,0	10,9
Combretum hereroense	—	14,3	30,0	—	—	36,8	8,7	26,0	13,0

*The number of headloads in which a species occurs as a percentage of the total number of headloads.

TABLE 5. — The proportion (as a percentage) of pieces of firewood in various diameter size classes

Family	Diameter 2,5 cm	2,6–5,0 cm	5,0 cm
1	51,6	32,8	25,6
2	53,6	32,2	14,2
3	71,2	19,0	9,8
4	54,2	34,0	11,8
5	51,4	41,0	7,6
6	62,0	29,2	8,8
7	47,8	33,7	18,5
8	53,6	31,2	15,2
Overall	55,8	31,2	13,0

3.2 *Building timber*

3.2.1 *Living-huts*

Of the 20 living-huts examined 4 were square structures, the remainder being round. One of the round huts was atypical in that it had no wooden framework to the wall. It was therefore omitted from the calculations.

The mean timber volumes for the round and square huts are: 1,22 ± 0,44 m^3 and 1,86 ± 0,6 m^3, respectively (Fig. 7).

The mean volume of wood in a living-hut is 1,30 ± 0,57 m^3.

The greater use of wood in square huts is reflected in Tables 6 and 7.

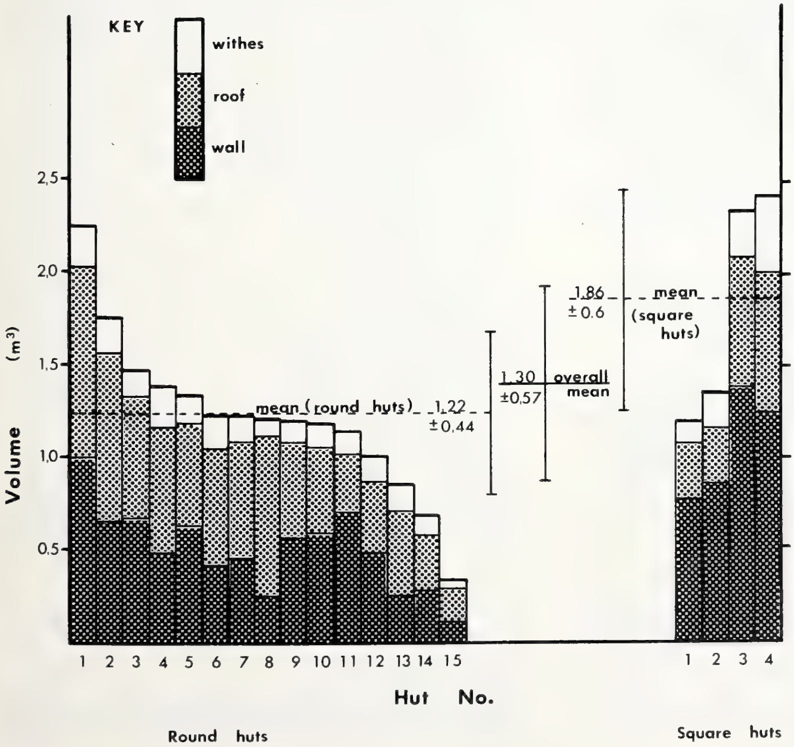

FIG. 7.— The volume of wood in the living-huts examined.

TABLE 6. — The average woody components and dimensions of a round living-hut

Hut circumference	16 m
No. of poles in wall	14
circumference of poles	41,0 cm
length of poles	280,0 cm
No. of primary poles in roof	17
circumference of poles	24,5 cm
length of poles	400,0 cm
No. of secondary poles in roof	14
circumference of poles	18,3 cm
length of poles	247,0 cm
No. of rows of withes in roof	15
circumference of withes	9,7 cm

Square living-huts generally have two rows of poles; one around which the wall is built and an outer row supporting the roof.

TABLE 7. — The average woody components and dimensions of a square living-hut

Hut perimeter	24 m
No. of outer support poles	13
circumference of poles	14,4 cm
length of poles	198,0 cm
No. of poles in wall	16
circumference of poles	47,6 cm
length of poles	263,0 cm
No. of primary roof poles	17
circumference of poles	24,4 cm
length of poles	433,0 cm
No. of secondary roof poles	33
circumference of poles	15,8 cm
length of poles	189,0 cm
No. of rows of withes in roof	20
Circumference of withes	12,4 cm

3.2.2 *Storage-huts*

These are of two types; storage-huts built on a floor raised 30–40 cm off the ground and those built on an elevated platform about 2 m off the ground. Only 3 of the 15 storage-huts examined were of the elevated type. Of the remaining 12, 2 were incomplete, having no roof. These were not included in the calculations.

The mean timber volume in the typical storage-huts was ± 0,3 m^3 (Fig. 8) and that of elevated storage huts was 2,36 ± 1,31 m^3.

The average woody components and dimensions of a typical storage-hut are given in Table 8.

3.2.3 *Numbers of huts built*

The statistics taken from the permit records at the Giyani magistrate's office (Table 9) show that a total of 89 living-huts, 80 typical storage-huts and 4 elevated storage-huts were built in the period April 1980 to March 1981, as well as 5 fences and 7 stockades. The wood used for these last two structures was not studied.

3.2.4 *Species used*

In the living-huts *Colophospermum mopane* accounted for 97,3% of the wood used. Other species are included in Table 10.

In storage-huts 92,2% of the wood used was *C. mopane* (Table 11).

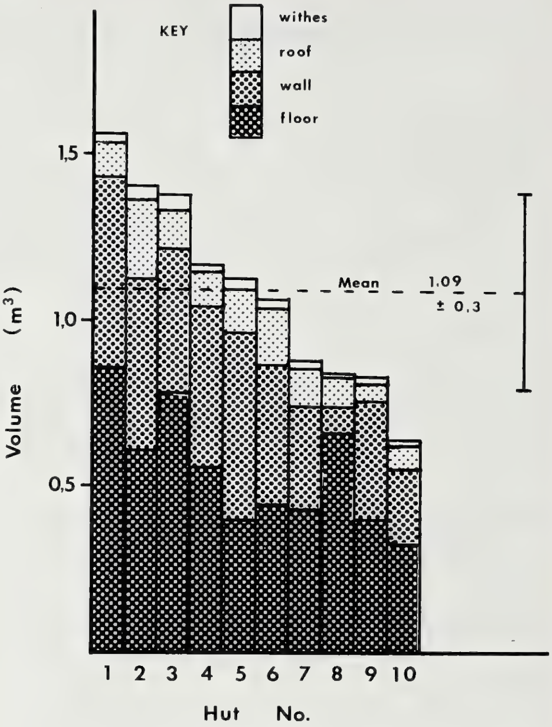

FIG. 8.— The volume of wood in the typical storage-huts examined.

TABLE 8. — The average woody components and dimensions of a typical storage-hut

Hut circumference	8,3 m
No. of support poles	3
circumference of poles	38,8 cm
length of poles	261,0 cm
No. of floor poles	41
circumference of poles	19,3 cm
length of poles	210,0 cm
No. of long wall poles	17
circumference of poles	22,6 cm
length of poles	198,0 cm
No. of short wall poles	109
circumference of poles	16,6 cm
length of poles	144,0 cm
No. of poles in roof	21
circumference of poles	16,7 cm
length of poles	234,0 cm
No. of rows of withes around wall	13
circumference of withes	8,4 cm
No. of rows of withes in roof	9
circumference of withes	7,7 cm

3.3 *Weather during monitoring periods*

Mean daily maximum and minimum temperatures were calculated for the monitoring periods from data obtained at the Giyani weather station (Table 12).

4 DISCUSSION

4.1 *Firewood*

4.1.1 *Consumption*

The number of families monitored was small in relation to the total present (8:978), but the results

TABLE 9. — Permits sold to cut wood for building. 1 April 1980–31 March 1981

Month	Village 1			Village 2			Village 3			Total		
	Living-huts	Storage-huts	Other*	Living-huts	Storage-huts	Other*	Living-huts	Storage-huts	Other*	Living-huts	Storage-huts	Other*
April	—	2	1	6	2	—	1	—	1	7	4	2
May	—	3	—	1	1	—	—	4	—	1	8	—
June	8	5	—	7	15/2**	2	4	2	—	19	22/2**	2
July	12	3	1	3	—	—	6	—	2	21	3	3
August	5	—	—	5	—	1	4	—	—	14	—	1
September	6	—	—	3	—	1	10	1	1	19	1	2
October	2	1	—	2	—	1	2	—	—	6	1	1
November	1	—	—	1	—	—	—	—	—	2	—	—
December	—	—	—	—	—	—	—	—	—	—	—	—
January	—	—	—	—	—	—	—	—	—	—	—	—
February	—	—	—	—	—	—	—	—	—	—	—	—
March	—	5	—	—	9/1**	—	—	31/1**	1	—	45/2**	1
Whole year	34	19	2	28	27/3**	5	27	38/1**	5	89	84/4**	12***

* The number of elevated storage-huts.

** Includes cattle stockades and fences.

*** 7 cattle stockades and 5 fences.

TABLE 10. — Woody species used in the living-huts examined, with their percentages of the total volume of wood used

Species	%
Colophospermum mopane	97,3
Acacia nigrescens	2,5
Combretum apiculatum	0,15
Combretum imberbe	0,05

agree with those by other researchers and probably give a reasonably accurate indication of firewood consumption under the prevailing conditions of almost unlimited availability.

Firewood consumption estimated for other areas of South Africa varies from as low as 1,5 tonnes per family per annum (Best, 1979) to 7,7 tonnes (Gandar, 1981). Consumption is apparently closely linked to availability. For relatively well-wooded areas Best's (1979) and Gandar's (1981) consumption figures are 4,8 tons and 7,7 tonnes per family per annum, respectively. In Zimbabwe, estimated firewood consumption in areas of high availability is approximately 5 tonnes per family per annum (based on the estimate of 8,44 m^3 per family per annum (Furness, 1979)).

The firewood consumption of 5,4 tonnes per family per annum estimated for this study area is comparable to that in other well-wooded areas.

Based on this figure, the total demand for firewood the 978 families in the study area is approximately 5 300 tonnes per annum.

4.1.2 *Seasonal variation in consumption*

The observed general trend to higher consumption in period 2, (August), is not explained by the weather data for the monitoring periods. The coldest weather was in period 1, June.

July/August is a time of initiation for the young girls and considerable quantities of sorghum beer are brewed for the celebrations, requiring additional amounts of firewood to that normally used.

It must be borne in mind that monitoring was discontinous and that peak firewood consumption for the year might have occurred between monitoring periods.

4.1.3 *Average weight of headloads*

The mean weight of headloads encountered during this study (29,95–31,64 kg) is considerably higher than those calculated by Best (1979) for his three villages, these being 21,3; 15,2; and 20,6 kg respectively. Whitlow (1979) gives the average headload in the Tribal Trust Lands of Zimbabwe as weighing from 24–36 kg. Jelenic & Van Vegten (1981), in their study of the firewood situation at Oodi in Botswana, found that headloads generally weighed 20–30 kg. In the present study approximately 60% of the headloads weighed 25–45 kg.

TABLE 11. — Woody species used in the storage-huts examined, with their percentages of the total volume of wood used

Species	%
Colophospermum mopane	92,9
Combretum apiculatum	6,6
Acacia nigrescens	0,5

TABLE 12. — Mean daily maximum and minimum temperatures during the monitoring periods (°C)

Period	Mean daily maximum	Mean daily minimum
1	23	7
2	27	10
3	26	14
4	29	20
5	29	19
6	24	14

4.1.4 *Heaviest headloads*

Few headloads weighed more than 50 kg and the heaviest load encountered (67,2 kg) was exceptional. Note: Bond (1977) refers to a headload weighing about 90 kg, but the heaviest loads recorded by Best (1979) were 32, 34 and 39,5 kg respectively for his three villages.

4.1.5 *Species used*

The two species most commonly collected as firewood, *Colophospermum mopane* and *Combretum apiculatum* are also the two species singled out in the initial interviews as being the best firewoods. This would seem to indicate that the people are selective in their gathering of firewood. These same two species are, however, also very common in the vegetation and their abundance in headloads could, therefore, simply be a result of their availability in the vegetation. An analysis of the vegetation would be necessary to determine whether, and to what extent, selectivity is being practised or not. There is considerable variation from one family to another with respect to what species are collected in quantity (Table 3). Some families (family 1 for example), collect several species in more or less equal proportions, whereas others (family 7 for example), concentrate on a single species. This may be determined by selective collecting as well as by what is available in each of the collecting areas visited by the families.

4.1.6 *Size of wood*

It is obvious that large-diameter firewood is not favoured by the women although it is available. Large wood requires splitting before use — unnecessary hard work if small wood is available. Small wood is also easier to break and to pack into a headload. An implication for woodlot management of this preference for small wood is that short-term coppice rotations would be feasible.

4.2 *Building timber*

The total volume of finished timber required for the 89 living-huts built in the study area in a year (calculated on the basis of a mean wood volume of 1,30 m^3 per hut) was approximately 116 m^3. For the 80 typical storage-huts built in the same period approximately 87 m^3 of finished timber was required and for the 4 elevated storage huts about 9 m^3.

These figures yield an overall estimate of 212 m^3 of finished timber used for building in a year.

From the data in Tables 6 and 8, it is estimated that some 21 000 poles of various lengths and circumferences were used to build the living-huts (assuming these all to be round) and the typical storage-huts.

Most of the wood used (95%) was *Colophospermum mopane,* the density of which (at 10% moisture content) is 1,09 g per cm^3 (Van Vuuren *et al.*, 1978). Using this as a conversion factor for all building wood, the total weight of finished timber used for building in a year was approximately 231 tonnes. This represents an annual timber requirement of approximately 230 kg per family.

There are no strictly comparable data on the use of building timber in rural areas. Gandar (1981) gives data on timber standing in structures in a homestead at any one time. In this study no data were obtained on the average number of living-huts and storage-huts per family but from observation each family appears to have two or three living-huts and a single storage-hut. The timber standing in structures in a homestead is, therefore, in the order of 2,60 to 3,90 m^3 for living-huts and 1,09 m^3 for storage-huts — compared to Gandar's (1981) figures of 3,08 m^3 for stores and kraals in lowland situations.

Few people in the survey area as yet buy *Eucalyptus* poles for building. *Colophospermum mopane* is more durable and insect-resistant than *Eucalyptus,* according to some people questioned. *Eucalyptus* poles are also expensive compared to the small fee payable (R1-00 to R3-00) for a permit to cut indigenous wood. In areas of critical wood scarcity, such as the Bungeni and Mbokota areas some 50 km west of Giyani, *Eucalyptus* poles are commonly used in building. The availability of this timber in nearby plantations in Louis Trichardt obviously influences the choice of building timber. In these areas the style of building is also affected by the shortage of wood. The walls of huts generally contain no poles, being made entirely of mud-bricks.

It is interesting to note that Gandar (1981) found a similar change in building strategy (i.e. from huts with wood in the wall to those without) in areas of low wood availability (upland situations).

4.3 *Demand versus supply of wood*

The annual demand for firewood and finished building timber in the study area as a whole, at the present rates of use, is approximately 5 500 tonnes. Assuming that this is all gathered from the 13 000 ha which are not residential or arable land, the rate of wood gathering is approximately 423 kg ha^{-1} $annum^{-1}$. Rutherford (1978) estimated the radial production of limbs and branches (i.e. wood production) for savannas and woodlands in southern Africa to be 600 kg ha^{-1} $annum^{-1}$, 177 kg higher than the above rate of use.

4.4 *Effects on the vegetation*

Observations on the effect of timber gathering on the vegetation showed the following general trends:

(a) cutting damage to trees, as indicated by stumps (coppicing or dead) and branches or stems cut off trees, decreases as one moves away from the perimeter of a village;

(b) the density of trees increases away from the village;

(c) shrubs tend to be smaller near the villages, usually less than 2 m in height, than they are further away, their height can be up to 3,5 m;

(d) in the highly disturbed areas (i.e. badly cut-out areas) the majority of the remaining trees have stems larger than 30 cm in circumference, whereas in less or little disturbed areas the majority of trees have stems less than 30 cm in circumference — ie. the smaller trees and stems disappear first; and

(e) there is no dead wood on the ground near the villages and very little further away.

These trends are not always equally clearly discernible and where they are present, the sequence or gradation is often disrupted due to clearing of land for cultivation, roads or pipelines. Other than the lack of fallen dead wood, the above effects are due to the cutting of building timber, rather than the collecting of firewood, and are very localized. The picture is accentuated by overgrazing and trampling of the grass and browsing of coppice and shrubs, as can be seen in Fig. 9.

4.5 *Possible role of woodlots*

At the present rate of use, harvesting of wood from the vegetation does not outstrip production, and harvesting on a sustained yield basis is feasible if:

(a) only the inhabitants of the villages utilize the wood resources of the study area, and

(b) If the wood is gathered evenly over the whole area. The people of the town Giyani, however, also make use of this resource at present. To supply these people with firewood and building timber and thus relieve some of the pressure on the vegetation of the study area, woodlots could be established around or near the town. The concentration of wood cutting and gathering in the immediate vicinity of villages is also wasteful as it leads to the elmination rather than the sustained harvesting of timber trees.

For the study area, management of the existing woodlands, together with the planting of trees in the denuded areas around the villages could ensure the continued supply of wood.

Fast-growing exotic species such as *Eucalyptus citriodora* and other drought-resistant eucalypts may be suitable (Wessels *et al.*, 1978). *Leucaena leucocephala* and a number of other leguminous trees also offer possibilities (National Academy of Sciences, 1980).

The introduction of exotics into the area should, however, be carefully considered, bearing in mind the aggressiveness and invasiveness of each candidate species and the threat it could pose to the natural vegetation, particularly along the rivers (Duggan & Henderson, 1982; Wells, Duggan & Henderson, 1980; Talukdar, 1981).

The feasibility of using indigenous species such as *Colophospermum mopane, Combretum apiculatum* or *Acacia* species needs investigating.

Fuel woodlots need only be managed on a short-term coppice rotation basis, since there is a preference for smaller wood for fuel.

5 CONCLUSIONS

Firewood is the major use for wood in the study area. It is estimated that the consumption of firewood is 5,4 tonnes per family per annum, similar to that measured in other parts of southern Africa with comparable availability of wood. Two species emerge as the most important sources of firewood — *Colophospermum mopane* and *Combretum apiculatum.*

The demand for building timber is 0,23 tonnes per family per annum. Almost all of the timber used is *Colophospermum mopane.*

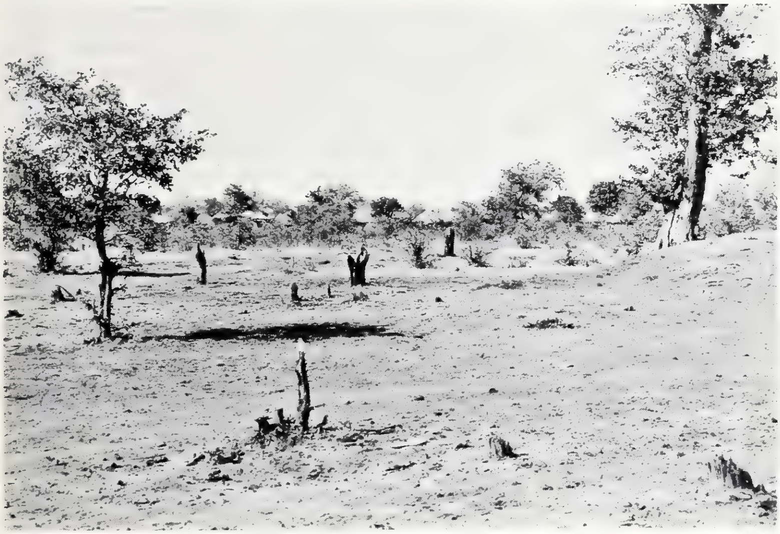

FIG. 9.— Denudation of the environment around a village.

Most of the live wood cut at present is for building: the obvious damage to the woody vegetation near the villages is, therefore, not due to the gathering of firewood but to the cutting of building timber.

Although the wood supply in the study area (and other adjacent areas) is adequate for the present needs of the local population, population increases, fuel gathering for adjacent towns, the escalating demand for agricultural land and wasteful harvesting methods result in the wood supply from indigenous vegetation becoming inadequate. Increased cutting of live wood for firewood will occur.

The establishment of woodlots of suitable exotic or, preferably indigenous species for fuel and building timber is required to prevent the complete destruction of the woodlands. Some parts of Gazankulu are already experiencing a shortage of

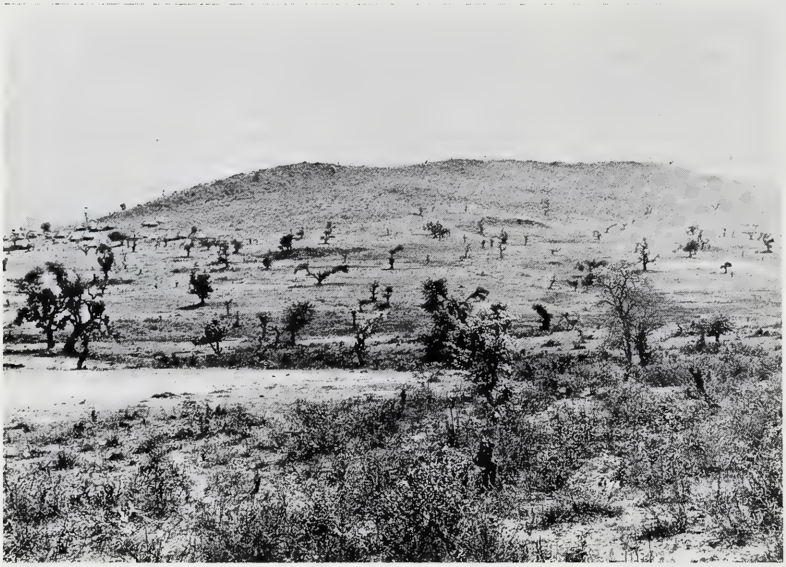

FIG. 10.— A part of Gazankulu already experiencing a critical shortage of firewood.

wood (Fig. 10) and small thorny shrubs, poor quality firewood, reeds and dung are burnt as fuel. Here, there is urgent need for the establishment of woodlots.

UITTREKSEL

Die benutting van hout vir brandstof en bouhout is oor 'n gebied van 13 000 ha. in Gazankulu, naby Giyani, bestudeer. Bondels vuurmaakhout wat deur 8 van die 978 families teenwoordig ingebring is, is gedurende 6 periodes in 'n jaar gemonitor.

Die twee belangrikste bronne van vuurmaakhout is Colophospermum mopane *en* Combretum apiculatum. *Die gemiddelde verbruik van vuurmaakhout per gesin per dag word bereken op 14,9 kg. Die jaarlikse aanvraag na vuurmaakhout in die hele studiegebied is gevolglik ongeveer 5 300 metrieke ton. Woonhutte en voorraadhutte is bestudeer terwyl dit in aanbou was. Die gemiddelde volumes hout in woon- en tipiese voorraadhutte is respektiewelik 1,30 m^3 en 1,09 m^3. Nege en tagtig woon- en tagtig voorraadhutte is in een jaar gebou. Die vraag na afgewerkte hout in die studiegebied in daardie jaar was ongeveer 231 metrieke ton.*

Houtverbruik het tot nog toe nie produksie oorskry nie, maar dit sal weldra gebeur indien alternatiewe houtbronne nie verskaf word nie.

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APPENDIX 1

WOODY SPECIES PRESENT IN THE STUDY AREA

(Voucher specimens housed in PRE)

Moraceae
Ficus sansibarica Warb.
F. sonderi Miq.
F. stuhlmannii Warb.
F. sycomorus L.
F. tettensis Hutch.

Urticaceae
Pouzolzia hypoleuca Wedd.

Annonaceae
Hexalobus monopetalus (A. Rich.) Engl. & Diels

Leguminosae
Acacia nigrescens Oliv.
A. permixta Burtt Davy
A. polyacantha Willd. subsp. *campylacantha* (Hochst. ex A. Rich.) Brenan
A. robusta Burch.
A. schweinfurthii Brenan & Exell var. *schweinfurthii*
Dichrostachys cinerae (L.) Wight & Arn. subsp. *africana* Brenan & Brummitt var. *pubescens* Brenan & Brummitt
Colophospermum mopane (Kirk ex Benth.) Kirk ex J. Leonard
Schotia brachypetala Sond.
Cassia abbreviata Oliv. subsp. *beareana* (Holmes) Brenan
Peltophorum africanum Sond.
Mundulea sericea (Willd.) A. Chev.
Ormocarpum trichocarpum (Taub.) Harms ex Burtt Davy
Dalbergia melanoxylon Guill. & Perr.
Pterocarpus rotundifolius (Sond.) Druce subsp. *rotundifolius*
Xanthocercis zambesiaca (Bak.) Dumaz-le-Grand

Balanitaceae
Balanites maughamii Sprague

Simaroubaceae
Kirkia acuminata Oliv.

Burseraceae
Commiphora mollis (Oliv.) Engl.
C. africana (A. Rich.) Engl.

Meliaceae
Turraea obtusifolia Hochst.
Trichilia emetica Vahl

Euphorbiaceae
Securinega virosa (Roxb. ex Willd.) Pax & K. Hoffm.
Pseudolachnostylis maprouneifolia Pax
Bridelia mollis Hutch.
Spirostachys africana Sond.

Anacardiaceae
Sclerocarya caffra Sond.
Lannea stuhlmannii (Eng.) Engl.
Ozoroa paniculosa (Sond.) R. & A. Fernandes
O. reticulata (Bak. f.) R. & A. Fernandes
Rhus gueinzii Sond.
R. leptodictya Diels

Celastraceae
Maytenus heterophylla (Eckl. & Zeyh.) N. Robson
M. senegalensis (Lam.) Exell
Cassine transvaalensis (Burtt Davy) Codd
Hippocratea longipetiolata Oliv.

Icacinaceae
Pyrenacantha grandiflora Baill.

Sapindaceae
Pappea capensis Eckl. & Zeyh.

Rhamnaceae
Ziziphus mucronata Willd. subsp. *mucronata*
Berchemia discolor (Klotzsch) Hemsl.

Tiliaceae
Grewia monticola Sond.
G. flavescens Juss. var. *flavescens*
G. flavescens Juss. var. *olukondøe* (Schinz) Wild

Malvaceae
Gossypium herbaceum L. var. *africanum* (Watt) J. B. Hutch. & Ghose

Sterculiaceae
Dombeya rotundifolia (Hochst.) Planch. var. *rotundifolia*

Flacourtiaceae
Flacourtia indica (Burm. f.) Merr.

Combretaceae
Combretum apiculatum Sond. subsp. *apiculatum*
C. collinum Fresen. subsp. *suluense* (Engl. & Diels) Okafor
C. hereroense Schinz
C. erythrophyllum (Burch.) Sond.
C. imberbe Wawra
C. mossambicense (Klotzsch) Engl.
Terminalia sericea Burch. ex DC.

Ebenaceae
Euclea divinorum Hiern
Diospyros mespiliformis Hochst. ex A. DC.

Loganiaceae
Strychnos madagascariensis Poir
Nuxia oppositifolia (Hochst.) Benth.

Apocynaceae
Carissa edulis Vahl

Boraginaceae
Ehretia amoena Klotzsch

Verbenaceae
Clerodendrum glabrum E. Mey.

Labiatae
Hemizygia elliotii (Bak.) Ashby

Rubiaceae
Breonadia microcephala (Del.) Ridsd.
Gardenia jovis-totantis (Welw.) Hiern
Tricalysia allenii (Stapf) Brenan
T. junodii (Schinz) Brenan var. *kirkii* (Hook.f.) Robbrecht ined.
Vangueria cyanescens Robyns
Pavetta schumanniana F. Hoffn. ex K. Schum.

APPENDIX 2

SPECIES COLLECTED AS FIREWOOD

Acacia nigrescens
Acacia sp.
Albizia harveyi
Berchemia discolor
Bolusanthus speciosus
Carissa edulis
Cassia abbreviata subsp. *beareana*
Cassine transvaalensis
Colophospermum mopane
Combretum apiculatum subsp. *apiculatum*
C. collinum subsp. *suluense*
C. hereroense
C. imberbe
C. paniculatum subsp. *microphyllum*
C. zeyheri
Dalbergia melanoxylon
Dichrostachys cinerea
Diospyros mespiliformis
Dombeya rotundifolia var. *rotundifolia*
Ehretia amoena
Euclea divinorum
Ficus sycomorus
Gardenia spatulifolia
Grewia flavescens
G. monticola
Lannea stuhlmannii
Lonchocarpus capassa
Maerua angolensis
Maytenus sp.
Mundulea sericea
Ozoroa sp.
Peltophorum africanum
Piliostigma thonningii
Pterocarpus rotundifolius subsp. *rotundifolius*
Schotia brachypetala
Sclerocarya birrea subsp. *caffra*
Securinega virosa
Strychnos madagascariensis
Terminalia sericea
Trichilia emetica
Ximenia caffra
Ziziphus mucronata

Bothalia 14, 2: 259–264 (1983)

Herbaceous standing crop in relation to surface and subsurface rockiness

M. C. RUTHERFORD*

ABSTRACT

A study, carried out in non-wooded parts of savanna and in desert grassland, demonstrated that herbaceous standing crop can decrease with increasing surface rock cover. However, such decreases corresponded more directly to a soil volumetric decrease than to a decrease in soil surface area *per se.* The relationship was also found to depend strongly on subsurface rock weathering patterns which may reverse the indicated relationship between standing crop and surface rock cover. The application of surface rock cover data without regard to profile stoniness, is, therefore, likely to be of limited use for comparing plant production across different geological substrates. The role of different rock types in giving rise to soils of different fertility with corresponding plant responses, was also indicated by the data. Sensitivity of plant standing crop to surface rock cover was possibly dependent on mean annual rainfall, but further data are required. The interpretation of aboveground standing crop data in terms of aboveground annual production is briefly discussed.

INTRODUCTION

Surface rock cover is a recognized environmental feature in ecology and is often routinely recorded in vegetation and agronomic surveys. Many ground surface areas of southern Africa have some degree of surface rock or stone cover. Most soils of the extensive western Transvaal bushveld, for example, are reported to be shallow and stony with bedrock frequently exposed at the surface (Van der Meulen & Westfall, 1979). Surface rock is a potentially important factor in the much-needed extrapolation of primary production data from the few, cost intensive natural ecosystem research sites. The relevant areas are not limited to Lithosols, but also include the wide variety of soil units in both the Stony and Lithic phases (FAO-Unesco, 1974). The potential role of surface rock cover as a source of soil dilution and additional water capture is known (Daubenmire, 1974), but quantification of the natural plant production response has remained relatively unresearched. Even less clear are the effects of changed soil water flow patterns in soil with subsurface stones. Some work (Coetsee, 1972) in western Transvaal 'klipveld', which is characterized by stony conditions, has indicated lower plant production than in other areas of the region. Lower herbaceous standing crop values were found on litholitic complexes than any of the other soil types studied in the south eastern Orange Free State (Herbst & Goosen, 1973–75). The 'true soil ratio' (the volume of soil sample minus volume of the fraction larger than 2 mm diameter all divided by volume of soil sample) has been reported to be important in explaining productivity in stony soils (Czarnowski, *et al.*, 1971).

To obtain initial data on relations between plant production and degrees of ground rockiness, a survey of aboveground standing crop of the herbaceous layer of selected non-wooded parts of savanna and arid areas was undertaken at the end of the growing season (March–April). Hypotheses to be tested were: does surface rock cover relate to herbaceous plant standing crop?; is the form of any such relation affected by the subsurface rock weathering characteristics, rock type and rainfall? The term surface rockiness in the present paper includes both exposed bedrock and separate stones from gravel size fragments (FAO-Unesco, 1974) and larger.

STANDING CROP AND ANNUAL PRODUCTION

The use of standing crop as main vegetation parameter in the present study requires consideration. It is important to distinguish between standing crop and annual production, but also as important to realize that under certain conditions in perennial grassland, the two can be numerically equal. Maximum (peak) standing crop of aboveground parts of grasses usually includes, at one point in a year, the mass of all living and dead standing and attached material, therefore excluding litter. Standing crop is conveniently and rapidly determined by clipping. Annual production of aboveground parts is often more relevant to other functional ecosystem studies, but is far more difficultly determined by clipping. This is because only new material must be assessed and, since all losses of this material, especially to invertebrate consumers and litter during the active growth season, must be accounted. The interpretation of annual production of perennial grasses from harvest data with the need to detect simultaneous mass increases and losses, is a widely recognized problem (for example, Coupland, 1974; Singh, *et al.*, 1975).

Usually, the underestimation of annual production by peak standing crop, owing to undetected mass losses, has been emphasized and many conflicting results have been obtained in efforts to estimate actual production using different combinations of harvested mass subsets. Less emphasis has been placed on findings that peak standing crop in older, perennial grassland, with accumulation of old material, generally over-estimates annual production. The two situations are illustrated by savanna grassland data of Grossman (1981) which indicate

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that in one year old grassland, peak standing crop was only 75% of a detailed estimate of production (taking the various loss factors into account), but that peak standing crop was 137% of annual production of older grassland (more than five years old). (In the present paper, age applies to aboveground material, usually regenerated from the plant base following fire.) It, therefore, appears reasonable to suppose the existence of an age between young and old perennial grassland where standing crop approximately equals annual production.

The interseasonal course of standing crop in ungrazed or lightly grazed perennial savanna grassland can be approximated from various data which indicate that the peak of harvestable material, formed in the current growth season, is approximately halved before the start of the next growth season (Rutherford, 1976; Grunow *et al.*, 1980) and that a half-life in the order of one year may be assumed for disappearance of carry-over (residual) dead standing material from each of the last few preceding seasons (Rutherford, 1976). Data (Grossman, 1981) for a one year old (aboveground material) perennial herbaceous layer sward indicated that production was 34% greater than the peak standing crop. Assuming that this actual production remains constant for at least the first few seasons of aboveground growth, this amount produced corresponds to a calculated aboveground standing crop of grasses between two and three years old.

The above approach is obviously approximate and can be influenced by different clipping heights, varying rainfall and possible grazing in previous growth seasons, increased difficulties in recognizing ages of older grasses, also in multi-aged swards, onset of moribund properties with suppression of production through self smothering, and many other factors. Under certain conditions, the approach can, nevertheless, be expected to assist in estimating actual production using limited and relatively simple field techniques. In the present study, the two to three year rule of thumb, derived above, was applied in areas of very light grazing over recent seasons.

METHOD

Three sites were selected along a mean annual rainfall gradient from about 560 to 100 mm in the western Transvaal and northern and north-western Cape Province. The Veld Types included were Other Turf Thornveld, Kalahari Thornveld and Namaqualand Broken Veld (Acocks, 1975). At each site, a single fenced camp was selected in which past grazing appeared to have been light and any localized grazing and other patchy management practices were minimal. On the two savanna (Thornveld) sites, there was an open scattering of shrubs but sampling was restricted to non-wooded areas at least 5 m distant from nearest shrub edges. Grasses were dominant and were typically perennial, aboveground parts two to three years old, not moribund but ungrazed over the last growth season, and, as far as could be ascertained, no more than lightly grazed over the previous one or two seasons. Details of each site are summarized in Table 1. Within each camp, a control area with no or little surface rock, followed by areas with medium and (except in one) high surface rock cover were taken

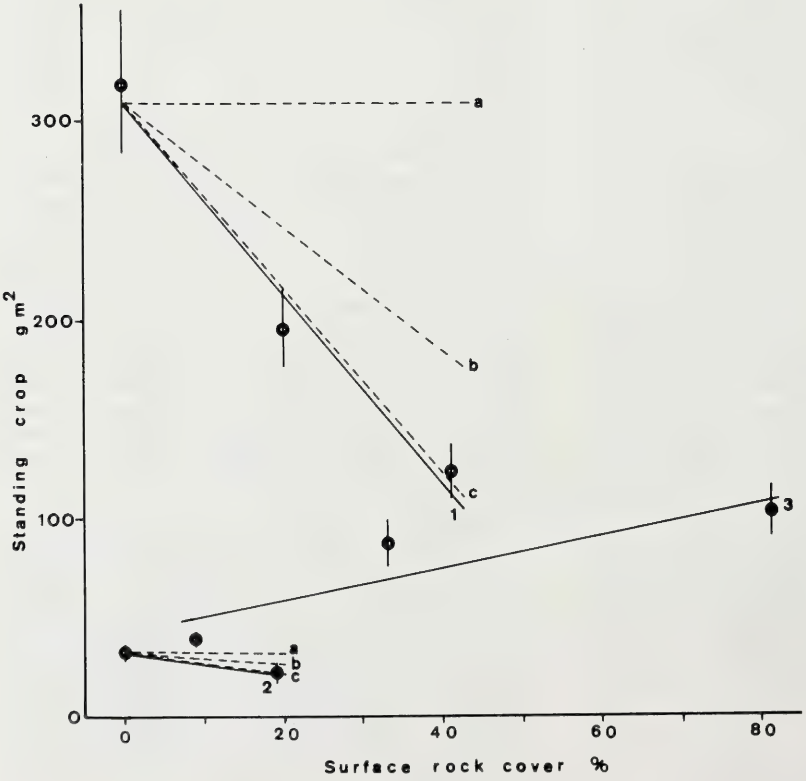

FIG. 1.—Relationships (by least square regression) between percentage surface rock cover and oven dry herbaceous standing crop for a: 1) relatively high rainfall Harzburgite site; 2) arid, transported sand site and 3) intermediate rainfall, sandstone/quartz site. Theoretically expected relations are: a) effect of runoff water capture balanced against soil surface reduction; b) soil surface reduction effect; and c) soil volumetric reduction effect. Bars represent ± one standard error of mean.

TABLE 1. – Herbaceous standing crop, percentage surface rock cover and qualifying data for three sites in open grassy parts of savanna and in desert grassland

Locality	Veld Type, No. and variations (Acocks, 1975)	Mean annual rainfall* mm	Topographic position	Dominant species	Rock type	Soil		No. $1m^2$ Quadrats	% Surface rock		Standing crop gm^{-2}	
						Texture	Colour		Mean	S.E.	Mean	S.E.
Brakfontein/ Marico (24° 57'S; 26° 13'E)	Other Turf Thornveld, No. 13	560	Bottomland	*Eragrostis rigidior* *Aristida meridionalis* *Rhyncheletrum repens*	Harzburgite	Loam	Red	10	0	0	319,3	36,7
			Midslope	*Diheteropogon amplectens* *Schizachyrium sanguineum*	Harzburgite	Loam	Reddish brown	10	20	3,2	194,1	19,5
			Upland	*Digitaria eriantha* subsp. *transvaalensis* *Heteropogon contortus* *Brachiaria nigropedata*	Harzburgite	Loam	Dark brown	10	41	3,3	122,7	14,2
Marthasrust/ Olifantshoek (27° 48'S; 22° 41'E)	Kalahari Thornveld, No. 16. Mixed Tarchonanthus – Rhus – Croton veld of the Langeberg	350	Bottomland	*Aristida congesta* *Stipagrostis uniplumis* *Eragrostis trichophora*	Quartz and sandstone	Fine sand	Yellowish reddish brown	20	9	2,0	38,5	3,8
			Upland	*Aristida vestita*	Sandstone and quartz	Fine sand	Light brown	15	33	2,9	86,8	12,3
			Upland	*Eragrostis curvula* *Aristida diffusa* *Brachiaria nigropedata*	Sandstone and quartz	Fine sand	Light brown	15	81	1,8	101,4	13,1
Korridor/ Boesmanpunt (29° 02'S; 17° 22'E)	Namaqualand Brokenveld, No. 33 False Desert Grassveld	100	Bottomland	*Stipagrostis ciliata* var. *capensis*	> 1,2 m deep soil	Coarse sand (transported)	Reddish brown	30	0	0	32,1	4,0
			Lower slope	*Stipagrostis ciliata* var. *capensis* *Eragrostis spinosa*	Gneiss	Coarse sand (transported) with concretions	Reddish brown	30	19	3,2	21,8	5,2

* Error margin probably ± 10 mm owing to unavoidable extrapolation.

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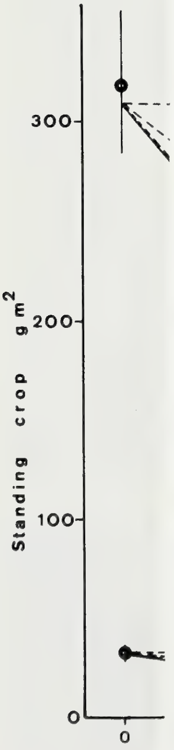

as sampling areas. Each camp spanned a land form from bottomland, through a slope to maximum rock cover near the top edge of a scarp. Microtopographic differences were taken into account to minimize the effects of different surface water flows from higher lying ground for each sampling area. One site was selected on basic igneous substrate (Harzburgite) to help reduce soil differences between sampling areas with different surface rock cover (J. L. Schoeman, pers. comm.). In many other rock types, different degrees of rock cover together with the commonly associated topographical differences, often result in different soil types that may confound the effect of the rock cover.

In each sampling area, one metre square quadrats were randomly placed and all plants were clipped at ground level, weighed to nearest 0,01 g and subsampled for dry mass determination by oven drying to constant mass at 85°C. Data on wet mass were used during sampling to estimate when standard errors approached, or fell below, 10% of the mean. Each quadrat's surface rock cover was estimated to nearest 5% and a series of standardized photographs was taken after clipping to check rock cover estimates by planimetry retrospectively. Profile pits were dug into the rock at each sampling area and profiles were photographed, details drawn, soil texture noted and rock samples taken for identification. It was found that profile stoniness was not readily quantified and that soil depth in many stony areas was not easily definable. Dominant plants of each sampling area were collected for identification by the National Herbarium, Pretoria.

RESULTS AND DISCUSSION

Results are summarized in Table 1. Standing crop was found to decrease with surface rock cover for the Harzburgite and arid transported sand sites but not for the intermediate rainfall, sandstone-quartz site (Fig. 1). Theoretically expected relationships include those where standing crop is linearly proportional to: 1) increased water runoff from surface rock (assuming no adhesion or evaporation) balanced against soil surface area reduction; 2) reduction in soil surface area only; and 3) reduction in soil volume only (proportionate reduction in soil depth with area) (Fig. 1). The first mentioned relationship provides a constant standing crop because the (simply proportional) increase through precipitation factor is the reciprocal of the decrease through area factor.

The data in Fig. 1 suggest that the standing crop on both the Harzburgite and arid transported sand may not depend primarily on possible increased moisture capture by surface stones or on surface rock cover *per se,* but rather on a reduction in soil volume. This was confirmed by the records of soil profile stoniness. The three Harzburgite sampling areas each had soil with plant roots down to at least 40 cm depth but with even, *in situ* weathering of irregularly rounded subsurface rocks throughout the profiles of the two rocky areas. Subsurface rock quantities were roughly proportional to surface rock cover. The arid transported sand site had deep sand (> 1,2 m) on the bottomlands and 10 cm deep sand deposited on gneiss with few fissures to 40 cm depth on the lower slope sampling area, again confirming a reduction in soil volume with increased surface stone. The steeper gradient of the above relationships in the high rainfall area than that found in the arid area (at least for the lower range of rock cover) may be explained by soil volume differences but may also reflect a reduced sensitivity of standing crop to surface rock in arid areas. This could relate to the effects of the much lower plant densities and greater spacing between individuals in the arid area and to more efficient utilization of some water capture by surface rocks in arid areas. Further investigation is needed. Extrapolation of the above relationships indicates that these are not linear over the whole range and that standing crop should decrease more gradually to zero at a point (determined mainly by minimum individual plant root system size) just below 100% rock cover.

The generally inverse relationship between surface rock cover and standing crop on the sandstone-quartz site is better understood when considered together with information from soil profiles of the site. The soil profiles of the three sampling areas of this site show distinct differences in patterns of subsurface rock weathering (Fig. 2). Rooting volume below about 10 cm deep was clearly inversely related to surface rock cover. These soil volumes at deeper levels may largely explain the inverse pattern found with the standing crop. The lack of a positive relationship between surface rock cover and effective soil volume here, brings into question the utility of surface rock cover as a single substrate parameter in evaluating standing crop in such areas. It may be necessary to restrict application of surface rock cover to certain geologically determined forms of soil genesis. A possible subsidiary factor that may have contributed to the standing crop patterns found on the sandstone-quartz site, is the possible lasting effect of past veld management patterns. Despite efforts to ensure limited and even past grazing treatment in the same camp during site selection, this area has a history of greatest grazing pressure on the bottomlands and lower slopes. The differences in plant species composition (Table 1) as veld indicators (Rattray, 1960) on this site also suggest that grazing has been heavier on the bottomlands in the past.

The standing crop (as defined), as indicative of annual production, on the relatively high nutrient status bottomland soils of the Harzburgite site was within 15% of an average prediction for 560 mm mean annual rainfall areas (Rutherford, 1980). However, production in all sampling areas of the sandstone-quartz area was more than 40% lower than expected and this difference possibly partly reflects the differences in nutrient status of soils on these two different geological substrates although other factors, including thermal effects (Rejmanek, 1971), are also possible.

ACKNOWLEDGEMENTS

The help of M. D. Panagos in all the fieldwork as well as the National Herbarium, Pretoria, for the plant identifications, is gratefully acknowledged.

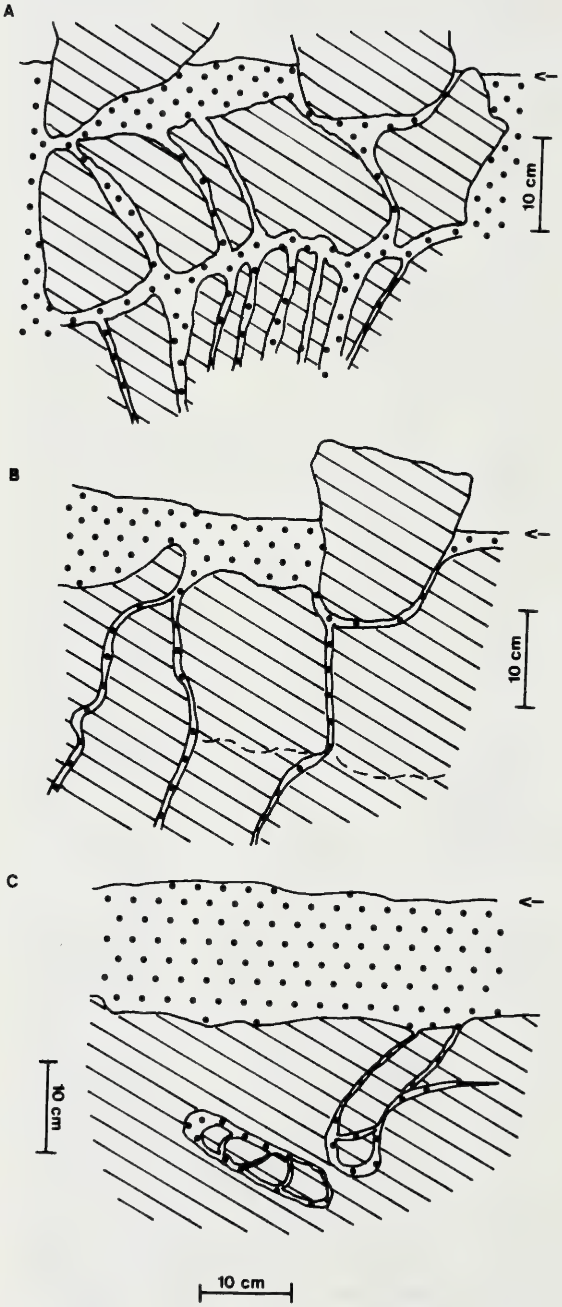

FIG. 2.—Soil profiles of sampling areas on the sandstone/quartz site, showing distribution of rock and soil in a) upland area with 81% mean surface rock cover and widely fissured bedrock; b) upland area with 33% mean surface rock cover and narrowly fissured bedrock; and c) bottomland with 9% mean surface rock cover with very little fissuring of bedrock. Rocks are lined and soil levels arrowed.

UITTREKSEL

'n Studie het aangetoon dat kruidagtige staande oes van oop gedeeltes van savanna en van woestyn grasveld kan afneem met 'n toename in oppervlakte rotsbedekking. Hierdie afnames stem meer direk ooreen met 'n afname in grond volume as 'n afname in die grondoppervlakte self. Daar is ook gevind dat die verwantskap ook op ondergrondse rots verweringspatrone sterk afhanklik is en tot 'n omgekeerde verwantskap mag lei. Die toepassing van oppervlakte rots bedekking sonder inagneming van profielklipperigheid, bleik dus om dikwels van beperkte waarde te wees vir die vergelyking van plant produksie tussen verskillende geologiese bodems. Die rol van verskillende rotstipes wat aanleiding gee tot gronde van verskillende voedingsgehaltes met ooreenstemmende plant reaksies, word na verwys. Sensitiwiteit van plant staande oes tot oppervlakte rotsbedekking is moontlik van gemiddelde jaarlikse reënval afhanklik, maar verdere navorsing word benodig. Die interpretasie van bogrondse staande oes in terme van bogrondse jaarlikse produksie word kortliks bespreek.

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Vegetation changes in the Hluhluwe-Umfolozi Game Reserve Complex from 1937 to 1975

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ABSTRACT

The structural changes that have occurred in the vegetation of the Hluhluwe-Umfolozi Game Reserve Complex have been quantified using 1937, 1960 and 1975 aerial photographs, and related to the management history. A progressive increase in both tree and shrub cover has occurred. In the short term, both intensive woody plant removal operations and controlled burning applications appear to be effective in retarding the rate of encroachment by shrubs and trees. However, neither was effective in the long term. Significant reductions in tall grass cover attributed to sustained overgrazing have occurred.

INTRODUCTION

A number of qualitative and semi-quantitative accounts of the vegetation of the Hluhluwe Game Reserve Complex have indicated that gross structural changes have occurred since proclamation (Henkel, 1937; Cowles, 1959; Deane, 1966; and Downing, 1972; 1980). This study was carried out in order to quantify these changes and to investigate their relationship to management practices.

THE STUDY AREA

The Complex (Fig. 1) is situated between latitudes 28°00' and 28°26'S and longitudes 31°43' and 32°09'E, the area comprises the Hluhluwe Game Reserve, the Corridor and Umfolozi Game Reserve and is 900 km^2 in area. It is divided into 34 game control blocks which form the framework for a continuous programme of ungulate population management. Five of these blocks were selected for this study (Fig. 1). Their environmental details are shown in Table 1. The general biogeographic features of this area have been described by Moll & White (1978). Acocks (1953) defined two major veld types present in the Complex, namely the Zululand Thornveld (type 6) which is a Coastal Tropical Forest type, and the Lowveld Tropical Bush and Savanna (type 10). The woody plant communities have been detailed by Whateley & Porter (1982).

METHOD

The 1937, 1960 and 1975 aerial photographs (respectively Jobs 117/37; 442 and 752 of the Trigonometrical Survey) of the five study blocks were adjusted by photographic transfer to a common scale of approximately 1: 20 000. Transparent sheets with a low light reflectance and super-imposed with a grid frame of 10 mm^2 units were placed over the photographs. A TOPCON stereoscope and a parallax bar were used to identify the vegetation at every grid point. The mean sample density for each block in all three years was one point for every 1,99 hectares.

The textural classes used were: (i) tree; (ii) shrub; (iii) tall grass and (iv) short grass and bare ground. Vegetation was identified principally on the basis of canopy height, e.g. woody components with canopies greater than 2 m in height were classed as trees, and those less than 2 m as shrub. Where vertical estimates were precarious because of poor

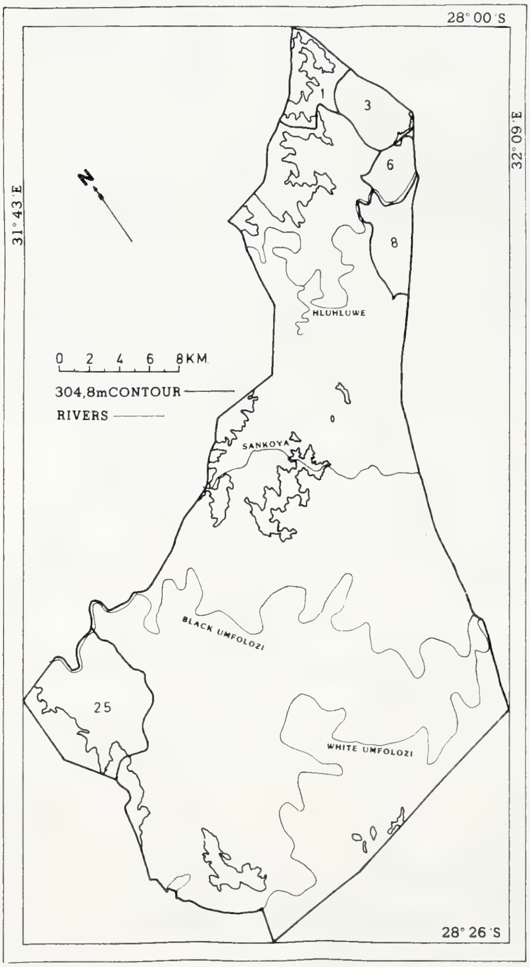

FIG. 1.—The location of the game removal blocks studied in Hluhluwe-Umfolozi Game Reserve Complex.

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TABLE 1.—Environmental features of study blocks

Game control blocks	1	3	6	8	25
Geology-listing in order of prevalence	Sandstone Shales	Basalt Sandstones Shales	Shales Sandstones Dolerite	Shales Sandstones Dolerite	Shales Sandstones Dolerite
Altitudinal range in m	122 to 495	122 to 390	82 to 390	152 to 497	122 to 598
Mean annual rainfall in mm	900	850	850	750 to 800	650 to 750
Bioclimatic sub-regions (Phillips, 1973)	9A, 9C	9A, 10B	10B	10B	9C
Total area in ha	1750	1656	965	1740	4960

photo resolution, identification was made on the basis of lateral canopy spread and similarity to other components of the same textural class previously identified on the basis of canopy height. The grass cover in areas identified on the photographs as having been recently burnt was classified as short. The percentage of each block occupied by each class was obtained by dividing the total number of points intercepting each class by the total number of grid intercepts examined, multiplied by 100, within each block.

Each group of ten adjacent points was treated as a sample unit. The number of points in each vegetation class was computed for each sample unit. The differences in this variate between the years studies were tested for statistical significance using the Standard Students t Test.

Summaries of the burning and intensive vegetation management histories for each block were extracted from annual maps lodged in the Hluhluwe Research Centre. The total area burnt each year within each block was measured for the period 1955 to 1974. Records prior to 1955 are not available. The 1975 fires occurred after the aerial photographs for that year had been taken. The burning data were summarized as the mean percentage of the area of block burnt per annum for the periods 1955 to 1959 and 1960 to 1974. The intensive vegetation management was of two main types: in block 25 a large strip was cleared of all woody vegetation as part of the anti-Tsetse fly campaign during the period 1942 to 1949 (Du Toit, 1954); in blocks 3 and 6 shrub invading areas of grassland and open savanna was selectively removed using a range of approaches over the period 1957 to 1969 (Ward, 1962). The areas treated were measured from maps and summarized as mean percentage of the area of each block treated per annum for the periods 1955 to 1959 and 1960 to 1974.

RESULTS

The results of the vegetation cover determinations are presented in Table 2. Derived parameters of vegetation change together with data on burning and intensive vegetation management within each study block are presented in Table 3.

The relationship between the rate of change in woody plant canopy cover and the mean percentage of the area burnt per annum is illustrated in Fig. 2. This relationship was shown to be significant at a 95% confidence level.

DISCUSSION

1. *Changes in tree and shrub cover*

A progressive increase in tree canopy cover over the period from 1937 to 1975 is apparent in each of

TABLE 2.—Vegetation cover percentages measured from aerial photographs

Game control blocks	1	3	6	8	25
Years	37 60 75	37 60 75	37 60 75	37 60 75	37 60 75
Tree	31 42 45	22 23 25	16 18 30	31 45 51	18 23 34
Shrub	14 25 27	41 56 55	44 61 58	12 30 37	51 44 30
Tall grass	30 12 18	37 21 18	39 20 12	35 15 7	29 31 33
Short grass + bare ground	25 21 10	0 0 1	1 1 0	22 10 5	2 2 3
Total woody plant cover	45 67 72	63 79 80	60 79 88	43 75 88	69 67 64
Trees as % of woody cover	69 63 63	35 29 31	27 23 34	72 60 58	26 34 53

TABLE 3.—Derived parameters of vegetation change together with data on burning and intensive vegetation management

Block	1		3		6		8		25	
Period	37–60	60–75	37–60	60–75	37–60	60–75	37–60	60–75	37–60	60–75
Vegetation:										
Change in % cover of woody plants/annum	+0,96	+0,33	+0,70	+0,70	+0,83	+0,60	+1,39	+0-87	−0,09	−0,20
Change in % cover of tall grass/annum	−0,78	+0,40	−0,70	−0,20	−0,83	−0,53	−0,87	−0,53	+0,09	+0,13
Fire:										
% of block burnt per annum	17	26	12	24	3	13	9	12	48	20
Intensive management:										
% of block cleared per annum	0	0	0,74	2,00	0	0,80	0	0	2,2	0

the blocks studied including the Umfolozi block where woody vegetation was completely cleared from 51% of its total area during the period 1942 to 1949. The range in tree canopy cover increase excluding block 3 is from 14% to 20%. The relatively small increase in block 3 of 3% may possibly be attributed to the woody plant removal operations which covered 17% and 30% of its area during the periods 1957 to 1960 and 1960 to 1969 respectively. These trends indicate that burning is not effective in the long term retardation of tree invasion.

Shrub invasion is effectively retarded by burning in the short term (MacDonald, 1980; 1981). However, the net increases in shrub cover over the period 1937 to 1975 in all four Hluhluwe blocks suggests that this control, even where it is supplemented with intensive techniques, is not effective in the long term.

The observed reduction in shrub cover over the period 1937 to 1975 in block 25 may possibly be attributed to the 1974 burn of 52% of its area following five years of virtual fire exclusion and an above average rain season. Such a burn may be expected to have reduced a large proportion of the shrubs to a ground level coppice (MacDonald, 1980) which would not have been detected in the 1975 photographs.

2. *Effectiveness of fire in limiting woody plant encroachment*

Burning is the major management tool employed in the Complex to arrest the encroachment of woody species as logistic considerations have always limited the extent and frequency of intensive operations (Table 3; MacDonald, 1980; 1981). Despite the repeated use of fire since the Complex's early history, there have been no previous quantitative evaluations of its long term effects.

In the Umfolozi block, a net decrease in the total woody plant cover over the entire study period occurred. This decrease was more pronounced during the 1960 to 1975 interval, presumably because of the large 1974 fire. Controlled burning within the Hluhluwe blocks over the study period did not effectively arrest or reduce the woody plant components. It may, however, have been instrumental in retarding the rate of woody plant encroachment (Table 3; Fig. 2).

The frequency of control burns appears to be too low for effective long term arrestment of the woody components. From 1955 to 1978 encroachment occurred throughout the Complex, although a mean of 23% of the total area was burnt each year (MacDonald, *et al.*, 1980).

This study indicates that in order to maintain woody cover at existing levels the mean percentage of the area that has to be burnt per annum is approximately 33%. This is equivalent to a burning frequency of once every three years. This estimate should however be regarded with caution, as it is

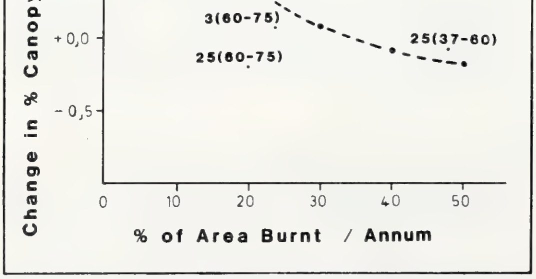

FIG. 2.—Relationship between rate of change in woody plant canopy cover and mean percentage of area burnt per annum.

derived from a period when data regarding the most effective frequency and season of burning was still accumulating. In particular many of the control burns were implemented after the first spring rains, a practice which is now considered to be deleterious to grasses and not as destructive to woody plants as a late dry season burn which is now being implemented. In addition, herbivore densities within the Complex between 1937 and 1975 exceeded the area's carrying capacity for extensive periods and therefore the fuel accumulation rates and hence fuel loads during burning, were probably too low on numerous occasions.

3. *Effectiveness of intensive operations in limiting woody plant encroachment*

During the 1940's the woody vegetation components were cleared from 51% of the area of block 25 in Umfolozi. The exact techniques employed in this area are not documented. In other areas cleared during the same campaign large trees were stumped out using a tractor, while smaller trees and shrubs were mattocked out at ground level and burnt in their felled positions. Although this clearing operation appears to have been effective in arresting the shrub encroachment, it had no long term effect on the encroachment of trees. As a result, the overall woody canopy cover on this block in 1960 was only 2% less than it had been in 1937.

The other block where large scale intensive management has been practised is number 3 in Hluhluwe. Although these operations apparently limited recruitment to the tree layer (*Acacia karroo* was the main species controlled and this species can form extensive stands of trees), the shrub cover increased considerably so that the overall woody canopy cover increased from 63 to 80% over the study period. The single large operation in block 6 when the shrub layer was removed from 12% of its area, was also unsuccessful in arresting the trend to woody plant dominance.

One of the reasons why this intensive management may have been ineffective is that the techniques used failed to kill the treated plants. This is highly likely in the case of the operations conducted in blocks 3 and 6: 408 ha were treated by cutting the plants at ground level, 328 ha by applying the arboricide 2-4-5-T to the plants and 150 ha by digging out the plant's rootstocks. Only the latter technique is likely to have resulted in anything like 100% mortality. The middle technique is influenced by such factors as concentrations, proportion of plants missed, season and method of application etc.; and has highly variable results, whereas the first technique is almost totally ineffective in killing those species treated.

4. *Changes in long grass cover*

In all the Hluhluwe blocks studied there have been signficant reductions in the extent of tall grass cover over the period 1937 to 1975. This has occurred notwithstanding the high proportion of short grass in two of the blocks in 1937 — thought to have been the result of an early dry season burn prior to the 1937 photography. The rate of decrease in tall grass cover in the Hluhluwe blocks was greatest in the 1937 to 1960 period. A possible reason for this is the fact that in Hluhluwe the first major reductions in grazer biomass were achieved in the late 1950's and 1960's.

In Umfolozi where block 25 actually registered an increase in tall grass cover over this early period, the anti-Tsetse fly game elimination campaign had reduced grazer biomass to very low levels over the period 1943 to 1953 (Du Toit, 1954). Most of block 25 was at this time outside the Umfolozi Reserve Boundaries and was a buffer zone in which total eradication of game was attempted. Game control was continued in this area over the period 1960 to 1975, and in fact large numbers of White Rhinoceros *Ceratotherium simum* were removed from the bush cleared zones due to the relative ease with which animals could be captured in these areas.

It appears then, that the long grass component of the study blocks has been reduced primarily through sustained overgrazing, a conclusion reached by other observers in the Complex namely, Cowles (1959) and Deane (1962).

5. *Consistency of results with other information*

The only previous attempt to quantify long term vegetation changes in the Complex is that of Downing (1980) who compared the 1937 and 1974 vegetation maps of Hluhluwe. However, due to differences in the mapping units used and the imprecision with which boundaries were determined these results are of questionable value. His estimate that 'grassland' areas decreased from 49 to 41% of the area during this period appears to be much too low. The comparable figures for areas covered by tall and short grass in the Hluhluwe blocks of this study are:- 55 to 28%, 37 to 19%, 40 to 12% and 57 to 12%. Most of this grass cover occurred within savanna communities. The accurate measurement of the area covered by vegetation communities in the Hluhluwe Game Reserve and northern Corridor, which is generally more open than Hluhluwe, showed that only 4% of the area was covered by grassland in 1975 (MacDonald & Phelan; in prep.).

In addition, Downing's (1980) findings that the increase in the extent of forest communities and the combined extent of woody communities of alluvial sand and lowland shrub communities over this period are 5% and 1% respectively, also appear to be gross underestimates. The results of this study and the comparison of historical photographs show an extensive displacement of lowland grassland areas by woody communities.

This study confirms Cowles's (1959) and Deane's (1966) reports of a decrease in the extent of tall grass communities and their replacement by shrubs in Hluhluwe over the period from 1925 to 1953 and in the adjacent Corridor over the period from 1954 to 1966, respectively.

Bourquin & Hitchins (1979) used the 1937, 1960 and 1969 aerial photographs to 'map apparent differences in the vegetation' of a study area in north western Hluhluwe. Although their results were not quantified, they concluded that there had been an increase in the area covered by woody plant communities between 1937 and 1969. From inspection of historical photographs, they concluded that 'Rapid development of encroachment in Hluhluwe started taking place after 1949'.

Ward (1962) views the open grassland in Hluhluwe as a seral stage of the vegetation which may be prevented from progressing towards its climatic and edaphic forest climax by being subjected to the periodic retarding influence of fires. Downing (1972), likewise, views the Umfolozi grassland as a subclimax community which is part of the Deciduous Woodland Formation.

Hall (1977) and Feely (1978) have proposed that the increased frequency of vegetal firing associated with human occupation which dates back to Palaeolithic times, served initially to reduce the proportion of woody communities present within the Complex, and thereafter to maintain the dominance of grassland communities.

Weisser (1978a; 1978b) and Weisser & Marques (1979) have indicated the duration of the seral stages towards the forest climax of the Coastal Belt of Northern Natal once human influences such as burning, clearing, shifting cultivation and cattle-grazing were prevented.

From the results of this study, it is apparent that grassland areas, particularly those created by clearing established woody vegetation, are rapidly invaded by woody plants. The reduced frequency with which the vegetation was burnt and the removal of other human influences following the reserves' proclamation is seen as a fundamental factor responsible for the recent increase in the Complex's woody plant communities.

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UITTREKSEL

Strukturele veranderings in die plantegroei van die Hluhluwe-Umfolozi Wildreservaatkompleks is bepaal deur lugfoto's van 1937, 1960 en 1975 met mekaar te vergelyk. Hierdie gegewens is gekorreleer met bestuurspraktyke in die reservate. 'n Toename in sowel boom- as struikbedekking het voorgekom. Op die korttermyn skyn dit asof die verwydering en beheerde brand van houtagtige species die uitbreiding van hierdie veldtipe voldoende vertraag. Op die langtermyn nie een was doeltreffend nie. 'n Aansienlike afname in langgrasbedekking het voorgekom wat kan waarskynlik aan voortdurende oorbeweiding toegeskryf word.

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Remote sensing and vegetation mapping in South Africa

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ABSTRACT

Effective use of remote sensing techniques for vegetation mapping and monitoring is a function of scale, resolution, season of imagery, kind of vegetation, sensor and spectral sensitivity, processing of the remote sensing product and speed and precision of transfer of information into a map product.

The kinds of imagery, types of data and general relationships between scale of study, scale of mapping and scale of remote sensing products that are appropriate to the South African situation for visual and digital analysis are presented. The type of remote sensing product and processing, the type of field exercise appropriate to each, and the purpose of producing maps at each scale are discussed. Lack of repetitive imagery to date has not allowed for the full investigation of monitoring potential and careful planning at national level is needed to ensure availability of imagery for monitoring purposes. Map production processes which are rapid and accurate should be utilized. An integrated approach to vegetation mapping and surveying, which incorporates the best features of both visual and digital processing, is recommended for use.

1. INTRODUCTION

'Remote sensing is the acquisition of physical data of an object without touch or contact' (Lintz & Simonett, 1976). Effective use of remote sensing techniques for vegetation mapping and monitoring is a function of scale, resolution, season of imagery, kind of vegetation, sensor and spectral sensitivity, processing of the remote sensing product, and speed and precision of transfer of information into a map product. The field of remote sensing has expanded over the past thirty years from the use of small scale panchromatic photographs taken from aircraft primarily for trigonometrical work, to a wide variety of remotely sensed products used in many disciplines and which are taken from various platforms ranging from helicopters to spacecraft.

The current awareness by planners and land-managers of the important role that vegetation plays in maintaining a stable environment has created a demand for vegetation mapping and monitoring at various scales. The majority of these surveys can be more efficiently and accurately done with the aid of remotely sensed products. However, although air photographs have been widely used as support products in vegetation studies in this country, there have been few published studies on the comparative effectiveness of different products for specific purposes, such as that by Jarman (1977) in the eastern Orange Free State, who compared the accuracy of air photo interpretation from panchromatic, colour and infra red false colour air photography. Most workers have had one film or remotely sensed product available to them or, at best, have been in a position to order a particular product because of prior knowledge of its effectiveness. This paper attempts to bring together information on various remote sensing products and their processing which would be relevant to vegetation science workers.

In any vegetation study the problem, or aims and objectives, must be clearly defined prior to embarking on the study, and especially before obtaining any remote sensing products. If a map is to be used to illustrate the results of a vegetation survey the amount of information to be gathered by fieldwork and from remote sensing media should be applicable to the final mapping scale. It is essential to understand the relationships and differences between the terms 'scale of survey', 'scale of mapping' and 'scale of remote sensing' (Küchler, 1967; Edwards, 1972a). The scale of remote sensing and mapping is entirely dependent on the scale of survey, which is dictated by the problem which has to be solved and how the results are to be presented. For purposes of convenience, vegetation surveys have been grouped into five major classes:

1. General and general-reconnaissance surveys
2. Reconnaissance surveys
3. Semi-detailed surveys
4. Detailed surveys and studies
5. Ultra-detailed surveys and studies
   (after, Edwards, 1972a & b, Edwards & Jarman, 1972).

It is implicit in the interpretation of remotely sensed products for vegetation mapping purposes that a classificatory process is involved (Webb, 1954). This emphasizes an important distinction between the approach of a vegetation mapper and a geologist mapping geological surface features. The geologist is trying to enhance images for *detail,* whereas the vegetation worker is aiming to simplify the detail into manageable categories — or classify ground cover types on certain criteria.

It is essential that the nature and requirement of the classificatory process being applied is clearly understood. For vegetation survey, the view taken here is that the properties of the vegetation should be the primary criteria for its classification. The chief vegetational criteria by which vegetation has been classified, singly or in combinations, are physiognomy, structure and dominance, floristic composition

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and successional relationships. Again, scale of survey, scale of mapping and scale of remote sensing product determine the classificatory process used. Non-vegetational criteria such as habitat and geomorphology are used where vegetation units may not be the prime consideration, such as in land use surveys and assessments for site potential.

When discussing scale in this paper, large scale includes scales of from 1: 20 000 to 1: 10 000 and larger, medium scale from 1: 20 000 to 1: 125 000, and small scale includes scales of 1: 125 000 to 1: 3 000 000 and smaller.

With the current availability of remote sensing products, use of which will be described in separate categories in the following account, it is highly recommended that an integrated approach to the use of remote sensing products be adopted. This implies a particular discipline and order in the collection and recording of all levels of data — from precise (co-ordinate identification) location of sample sites in the field, corresponding location of field sites on remote sensing products, choice of size of sample unit (it might well be necessary to take a series of nested samples), recognition of the level of detail to be collected at different scales, use of different products or processing throughout an area in order to emphasize different features of the area, and storage of data in a grid system which could be used by other workers in a variety of disciplines. It is also necessary that nationally acceptable and applicable classification systems should be adopted for describing extant vegetation or land cover samples. There has recently been a system devised for the structural characterization of vegetation in the Fynbos Biome (Campbell *et al.*, 1981), which has produced encouraging results when compared to vegetation map units produced by classification of Landsat imagery in the Langebaan area (Jarman & Jackson, 1981) and by Edwards (1983).

2. REMOTE SENSING MEDIA FOR VEGETATION SURVEYS

The procedure adopted in producing a vegetation map can be broken down into three basic steps: data collection, interpretation and product generation (Fleming & Hoffer, 1977). Two basic approaches to vegetation mapping are the image oriented system and the numerically oriented system (Landgrebe, 1973). Both approaches utilize data collected from a remote location. Aerial photography is usually obtained from aircraft altitudes, optimizes spatial resolution, and is recorded on photographic film. Multispectral scanner (MSS) data are recorded and stored in digital or analog format on computer compatible tapes. Temporal and wave-length characteristics are optimized and data are collected from both aircraft and satellite altitudes.

2.1 *Photo products for visual interpretation*

2.1.1 *Panchromatic prints*

South Africa has complete aerial photographic coverage in panchromatic film at scales from 1: 20 000 to 1: 75 000. These photographs are available from the Director of Trigonometrical Survey Office in Pretoria. Photographs of this type are used primarily for trigonometrical work, but have also provided a basis for most vegetation mapping carried out with the aid of remote sensing media in South Africa. Panchromatic photographs are not as efficient, or as accurate for some interpretation projects as certain other media, but these have often to be used in the absence of more suitable media. With good tonal contrast the human eye is able to distinguish 200 tones of grey.

2.1.2 *Infra-red black and white prints*

Another air photograph product in black and white print form is the modified infra-red photograph. This film is sensitive to near infra-red wavelengths (i.e. 0,83−1,1 microns) as well as the visible wavelengths, but not thermal infra-red. If only infra-red wavelengths were recorded, shadows would be black, whereas detail in the shadows is visible in modified infra-red with red and green light present and blue excluded by a filter.

Objects with high infra-red reflectance, such as plants which reflect infra-red from the cellulose cell walls (Blythe & Kurath, 1968), show up in light tones, whereas objects with high infra-red absorption, especially water, show up black, making this medium ideal for mapping vegetation in swampy areas. Black and white infra-red photography was used extensively for forest inventories in North America, before more sophisticated media became available, as the different types of timber trees could be recognized by their differing infra-red reflectance signatures (Jensen & Colwell, 1949; Schulte, 1951; Stellingwerf, 1969). Successful vegetation studies were also made using black and white infra-red photography (Ives, 1939; Schulte, 1951).

Useful qualities of infra-red films are its penetration of haze and its detection of free water surfaces which show up pitch black (Spurr, 1960). Haze penetration is of particular importance in tropical areas where atmospheric moisture decreases the clarity of normal panchromatic photographs.

2.1.3 *Colour aerial photographs*

Experiments carried out overseas produced conflicting results about the advantages gained from the use of colour prints for vegetation studies. Mott (1966), Anson (1969) and Goodier & Grimes (1970) all state that colour photography gives no added information over panchromatic photography for vegetation studies, whereas Becking (1959) and Heller *et al.* (1964) found colour to be advantageous. Goodier & Grimes (1970) suggest, however, that not enough basic research has been done to show final conclusions.

Colour has been tried and proved useful. Its major advantage lies in assisting interpreters who do not have a wealth of experience, as they are able to recognize patterns on hue as well as on textural differences and site factors, and not merely on slight tonal variations, textural differences and site factors as in the use of panchromatic products (Duddek, 1967). The eye can detect 20 000 different hue variations compared with a mere 200 tonal variations (Evans, 1948). Photo hues also correspond closely to the actual vegetation colours on the ground, which facilitates recognition of species. The disadvantages of this film type are that flying conditions, due to its inability to penetrate haze, and the processing, are more critical than panchromatic film and the cost is higher.

Colour transparencies have better resolution than colour prints (Welch, 1968) and, possibly, colours are more readily standardized as there are fewer processing steps. Transparencies, however, are inconvenient for fieldwork as they require a light table for viewing and annotation is more difficult. A field apparatus for viewing transparencies has, however, been described by Wear (1960). The major disadvantages with this product are that there is no negative master copy so that the transparencies cannot be easily duplicated.

2.1.4 *Colour infra-red*

Colour infra-red photographs, also termed 'false' colour photographs, record the same wavelengths as the black and white infra-red, but different dyes in the film are sensitive to the different wavelengths which create different hues on processing (Smith, 1968; Stellingwerf, 1969). Hues on this medium represent the following hue image features on the ground. The red image colours on the photographs represent objects on the ground with high infra-red reflectivity, such as active vegetation; ground features with red and green hues are represented by green and blue photograph image hues respectively, whereas objects with blue hues are excluded from the image by using a blue filter.

The use of the longer wavelengths improves haze penetration, which gives photo images sharp boundaries, thereby improving resolution and making this medium useful for detailed work. Because of its haze penetration properties, this film can be used to great effect in high level photography (Pease & Bowden, 1969; Pease, 1970).

Colour infra-red film has been claimed by overseas workers to be ideal for vegetation studies (Anson, 1969; Colwell, 1967; Driscoll, 1971). Anson (1969) claimed that twice the detail could be retrieved on this type than from panchromatic or even colour film. The use of this film medium is claimed by Lauer (1968) to decrease interpretation time by 25%, whereas Haack (1962), after statistical analysis was not convinced of the overall advantage of this medium. The various claims for this film type cannot be evaluated unless the particular problem for which it is to be used is clearly defined.

2.1.5 *Multi-spectral photography*

A comparatively new product is multi-spectral photography described by Yost & Wenderoth (1968) and Smith (1968). Light reflected from various objects is recorded by wavelength separately on black and white film. The separation of light into the various wavelengths is done by using a number of lenses each with a different filter combination. Pictures are then reconstituted by superimposing the different black and white transparencies. Being able to select the various wavelengths to be recorded makes this an extremely versatile medium (Malila 1968; Ross, 1971).

The multi-spectral approach has great potential for analysing vegetation and recognizing vegetation patterns, and has been used in a number of studies. The Landsat series utilizes a multi-spectral system as one of its two systems for recording data.

Depending on the scale used, this type of remote sensing can detect individual species (Weber, 1966), or make inventories of large areas (Lent & Thorley, 1969). This process is available in South Africa, but has not been used for general vegetation mapping from aircraft levels of resolution apart from brief experimental natural resource studies of vegetation.

Multi-spectral satellite products from Landsat 1, 2 and 3 in the form of single wave band black and white prints, black and white negatives, 3-band false colour composites, and 3-band false colour transparencies are all available at any suitable scale of any specified portion of a Landsat scene (185 × 185 km) from the Satellite Remote Sensing Centre (SRSC). The standard products of a whole Landsat scene (185 × 185 km) are issued as 1: 1 000 000 scale, 1: 500 000 scale and 1: 250 000 scale products (18,5 cm, 37,0 cm and 74,0 cm sizes) (Anon., 1982).

2.1.6 *Other photographic media*

Other remote sensing products include K-band radar (Morain & Simonett, 1967; Lewis & Waite, 1973) and thermal infra-red imagery (Colwell, 1967; Sabins, 1973). Neither of these have been successfully applied to vegetation mapping and appear better suited to geological applications.

The 1: 10 000 black and white ortho-photo product produced by the Directorate of Trigonometrical Survey is also available for specific areas. These are maps produced from 1: 30 000 scale black and white photos. They are paper products, not available as stereopairs, but have contour intervals of 5 m drawn in on them. For areas where they are available, they are an asset to field location of sites and are generally a practical product to use in the field.

2.2 *Digital imagery for computer-aided analysis*

The international emphasis in the use of remote sensing imagery for mapping purposes has swung away from purely visual or image oriented interpretation of data, to numerical, computer assisted classification techniques. These fall within the general heading of digital image processing.

Image processing can be regarded as any operation carried out on an image once it has been recorded on some medium. Recording of spectral reflectance from a portion of the electromagnetic spectrum in digital form allows for flexible manipulation of data with the aid of computer processing techniques. Digital image processing comprises three main branches:

1. Image restoration processes which recognize and compensate for data errors, 'noise' and geometric distortion introduced in the scanning and transmission processes.
2. Image enhancement processes which modify an image in order to alter impact on the viewer.
3. Information extraction processes which utilize the decision making capability of computers to

identify and extract specific groups of information (Sabins, 1978).

Visual interpretation of imagery in the form of photo products is equivalent to information or feature extraction processes when applied to digitally stored spectral information.

The information extraction processes use computer classification techniques on two or more bands of multi-special scanner (MSS) digital data. Processing of the multi-band image is made possible by recognizing and classifying the spectral signatures in their numerical form. Each picture element (pixel) is assigned to a specific class by matching the spectral signature with the range of signatures determined for the class. The preprocessing leading up to the classification is geared toward locating and identifying representative groups of signatures, called training classes, and ensuring that they are sufficiently different to prevent confusion among them. This type of pattern recognition in digital image processing is statistical in character, and includes 'statistical space' in which the 'pattern' is a vector made up of a number of measurements in an n-dimensional space, where n represents the number of MSS bands utilized. The pattern recognition system seeks to partition or place boundaries in the n-dimensional space so that each region of the image can be assigned to a class of patterns (Hajic & Simonett, 1976). A mosaic of the image may thus be simplified into n manageable number of relatively homogeneous spectral classes.

2.2.1 *Landsat computer compatible tapes*

Since January 1981, Landsat imagery has been directly received in digital form on computer compatible tapes (CCT's) at Hartebeeshoek Satellite Remote Sensing Centre. Digital imagery dating back to 1972 when the first Landsat satellite (ERTS−A) was launched is also obtainable from the Satellite Remote Sensing Centre and from NASA. MSS Landsat data are recorded in four bands on computer compatible tape for the pixel units (picture element 56 × 79 or 0,44 ha). The wavelengths of the bands are:

Band 4 (Green)	0,5−0,6μ
Band 5 (Red)	0,6−0,7μ
Band 6 (near 1 R)	0,7−0,8μ
Band 7 (near 1 R)	0,8−1,1μ

Processing of this digital imagery is being carried out for vegetation, land cover and land use mapping purposes at the Satellite Remote Sensing Centre; at the National Physics Research Laboratory (NPRL), Council for Scientific and Industrial Research (CSIR), using the VICAR system on an IBM system 370/158 (Fink & Van Zyl, 1977); at the University of Cape Town on a UNIVAC 1100 Model 18 Computer (Anon., CATNIPS and NEWPIPS); and at the University of Natal on a UNIVAC Computer (Anon., NEWPIPS).

2.2.2 *Digitized air photos*

The Satellite Remote Sensing Centre has facilities for digitizing standard air photos on request. This is done by scanning the photo with a scanning microdensitometer and recording the grey scales from black and white imagery, or colour intensity on other imagery in digital form. Scogings & Ward (pers. comm., 1981) are involved in a vegetation study of the Kuiseb River region, using imagery which has been processed in this way. All the techniques of digital processing carried out on Landsat products are relevant to these digitized products. They provide a superb interface between satellite imagery and air photos, and between visual interpretation and computer analysis feature extraction processes.

3. SEASON OF IMAGERY — TIMING OF PHOTOGRAPHY

As maximum information on remote sensing imagery is associated with maximum contrast on the ground, remote sensing products should usually be made at the time of maximum vegetal contrast on the ground. This time of contrast varies, depending on climate and structure of the vegetation.

In grassland in South Africa, maximum contrast in the visible wavelengths would be in the autumn period of March, April and May, when the different grass species take on their autumn colours prior to being bleached by the winter climate. Similar results are reported by Driscoll (1971) in America. The exact time for ideal photography will, however, vary from year to year depending on local variation in the rainy season.

If it were necessary to take the imagery at a less favourable time, such as during mid-summer when all grasses appear a uniform green, it is possible to change the remote sensing medium from, for example, colour prints to infra-red colour prints, or to multi-spectral photographs where the difference in species could possibly be detected using additional infra-red wavelengths or a particular section of the electromagnetic band. If, however, the aim were to detect shrubs and trees in open woodland, remote sensing products should be made when contrast between shrubs and trees and grass is maximal, which would probably be prior to the trees losing their leaves, when perhaps the grass is dying back, or after the first flush of spring, when the tree leaves are green, but the grass still has its winter yellow colour.

Repetitive imagery from Landsat 1, 2 and 3 has shown the effect of seasonal change in obscuring or enhancing certain patterns in the landscape. In summer imagery over the summer rainfall region of South Africa, vegetative growth masks certain cultural features, yet enhances some geological features. In winter, evergreen vegetation is clearly separated from seasonal vegetation, whereas in summer the differences are less marked due to lower contrast. The timing of imagery is therefore dependent entirely on the aim of the particular project.

Work by Jarman (1981) on digital Landsat imagery in the Langebaan area, and by Lane (1980) on digital Landsat imagery in the Verlorenvlei area, has revealed an interesting aspect of the importance of seasonal variation. With good cover (>70% projected canopy cover) for West Coast Strandveld

(Acocks's Veld Type 34) communities in the Langebaan area, summer imagery provides greater distinction between the drought deciduous elements (losing leaves in summer) and the evergreen elements. However, further north at Verlorenvlei, as the ground cover drops to values of 5–25%, summer imagery containing the drought deciduous elements gives no distinction from the background soil characteristics. It would appear that in the lower cover categories (below 50% ground cover), the time of maximum leaf standing crop is the best time for vegetation mapping. In good ground cover areas (>50%) the time of maximum contrast between dominant elements should be chosen.

Time of day at which imagery is taken is also important. Careful selection of sun angles can utilize shadow to enhance features. Photographs taken at midday in some areas can also introduce a haze problem. The Landsat satellite orbit is sun-synchronous and the satellite passes over a particular area at the same time of the day at each pass. However, throughout the year, the sun angle is changing all the time. Repetitive Landsat imagery, therefore, can reveal or enhance certain features because of the changing sun angle. This is an advantage when it comes to enhancement for feature extraction purposes, but a disadvantage when change detection is the main objective.

4. SCALE OF SURVEY, SCALE OF MAPPING AND REMOTE SENSING

Küchler (1967) stresses the relationships between the scale at which the survey is planned, the final mapping scale and the scale of suitable remote sensing products. Different scales of survey will detect different types and sizes of vegetation pattern. The survey scale hence indicates the degree of precision at which the vegetation is studied, recognized and described. Table 1 is not intended as a rigid system, but is a suggested system relating these three factors. The major groups of scales of survey with their inherent restrictions as to field methods of vegetation analysis and scale of remote sensing products are presented.

Scale of remote sensing products is usually larger than the mapping scale. The remote sensing product contains more information than is actually required on the map. The scale difference is in order to make boundaries as accurate as possible. It does mean, however, that for mapping much of the information on the remote sensing product has to be classified into major types to make the map easily intelligible.

The classing of survey scales given in Table 1, based on Edwards (1972b), is one of many similar classifications. However, it has been designed for specific use in South Africa. It is appropriate to visual interpretation of photo products. Table 2 (from Jarman, Bossi & Moll, 1981) relates to the use of computer classification procedures as applied to Landsat digital imagery. It gives a breakdown of selected scales of mapping based on Table 1, giving the minimum size of map unit recognized at each scale and what this means in terms of the number of pixels involved in classification in each instance.

In the Jarman, Bossi & Moll (1981) study involving computer classification of digital data it was decided to limit investigation to four scales of operation, namely:

1. detailed (1: 10 000)
2. semi-detailed (1: 20 000)
3. semi-detailed (1: 50 000)
4. reconnaissance (1: 250 000)

These four scales of operation were selected because of the availability of maps, standard air photo products, and orthophoto products at these scales.

TABLE 1.—General relationship between scale of study, scale of mapping and scale of remote sensing product using visual interpretation techniques (after Edwards & Jarman, 1972)

Scale of survey	Aim	Final map product scale	Appropriate air photo	Appropriate field sampling procedures
General and General Reconnaissance	Ascertain major classes of vegetation at regional and sub-regional landscape levels	1: 1 000 000 or smaller	1: 500 000 – 1: 1 000 000	Descriptive, non-defined, non-regular samples usually recording physiognomic types
Reconnaissance	Determine the main plant communities/ecological relations within regions or sub-regions	1: 50 000 – 1: 1 000 000	1: 40 000 – 1: 500 000	Non-regular samples, low density of plot samples recording structural types and dominant floristics
Semi-detailed	Investigation of physiognomic /structural and floristic structure of communities and habitat relations	1: 10 000 – 1: 50 000	1: 5 000 – 1: 20 000	Defined samples, moderately high density, recording structural types and total floristics
Detailed	Study of structure and function of community or part of community	1: 500 – 1: 10 000	1: 5 000 or larger	Intensive quantitative sampling on defined plots
Ultra-detailed	Study within community species/species group / habitat relations	1: 500 or larger	1: 500 or larger	Intensive quantitative sampling on defined plots/ species

TABLE 2.—Relationships between map scale, smallest recognizable map unit (in ha) and number of spectral units used in numerical classification of digital remote sensing data (from Jarman, Bossi & Moll, 1981)

Final map scale	Smallest map unit recognized = 2 print characters		Units used in digital classification	
	No. of pixels	(ha)	No. of pixels	(ha)
General and general reconnaissance >1: 1 000 000	3 200	1 408,0	1 600 (40 × 40)	704,0
Reconnaissance 1:250 000	200	88,0	100 (10 × 10)	44,0
Semi-detailed 1: 50 000	8	3,5	4 (2 × 2)	1,8
1: 20 000	2	0,8	1	0,4
Detailed 1: 10 000	1	0,4	1	0,4
Ultra-detailed <1: 500	Beyond the limits of resolution of current Landsat series			

4.1 *General and general reconnaissance surveys*

The purpose of these surveys is to ascertain the major classes of vegetation at regional and sub-regional landscape levels and the main climatic, soil and biotic relationships (biomes). Major extensive functional processes prevailing in the ecosystems involved, such as the main plant successional trends, or retrogressions, leading to prevailing climax, sub-climax and disclimax types would be identified. These surveys are based on either general observational data or on indeterminate stand data, that is, sample plots without a specific size, such as those in Acocks's method (Acocks, 1975). Mapping scales used to show the distribution of vegetation are at 1: 1 000 000 or smaller. The value of such surveys is for general and regional planning and for determining problem areas requiring further investigation. The map products would be prepared for those in the planning and administration levels.

For such surveys the obvious choice of remote sensing scale to detect the main landscape vegetation patterning is small, of the order of that obtained by high altitude, ultra wide angle photography and satellite imagery. Photo scales used are therefore 1: 500 000 or smaller.

At these scales, stereoscopic coverage is often not possible. The Landsat Return Beam Videcon and MSS do overlap sideways sufficiently for stereoscopic viewing (Lintz & Simonett, 1976). Stereoscopy at this scale, however, is often not required as these images are required only as mosaics.

The remote sensing medium, by nature of the distances involved between 'sensed' surface and recording surface, must be highly sophisticated, and the accepted forms are multi-spectral imagery as well as active and passive radiometric methods, of which the images may be displayed in the form of a computer print-out.

The application of computer classification techniques to compress Landsat digital data at this scale would not be suitable. Compressing information into 40 × 40 pixel blocks at a 1: 1 000 000 scale of operation would lose too much information (Jarman, Bossi & Moll, 1981).

Maps resulting from these surveys, at scales of about 1: 1 000 000, cover large areas and delimit major vegetation types. The usual approach to this type of mapping would be either from combining information from larger scale maps or from photographic images at extremely small scales, such as the photographic imagery from Landsat 1, 2 and 3, which is commonly available at a scale of 1: 1 000 000.

The only vegetal detail to be considered at this level would be gross physiognomic types, which are often associated with major geographical divisions as expressed by Drued (in Cain & Castro, 1959) for example, equatorial forests and monsoon forests, or recognizing only the vegetation formation types like forest (Fosberg, 1961). These vegetation maps are not based on detailed fieldwork. African maps produced for these purposes include the AETFAT Vegetation Map of Africa, South of the Tropic of Cancer (Keay, 1959), at a scale of 1: 10 000 000, and a map at a scale of 1: 4 000 000 by Pole Evans (1936) of the Vegetation of South Africa.

The best known map of the vegetation of South Africa is that by Acocks (1975) at a scale of 1: 1 500 000. This map represents an exception to the general rule for surveys at these scales, as the vegetation classification is based on floristic data and site type criteria from 'samples' which provides unusual detail at this level of survey. On every landscape type, or area within the same farming potential Acocks (1975) recorded all the species present and their abundance, and on this his Veld Types were based. In this case, the information was initially mapped at 1: 500 000 and then reduced to 1: 1 500 000 to give a more concise picture and a more practical and manageable map.

4.2 *Reconnaissance surveys*

The purpose of these surveys is to redefine and confirm more accurately the main classes of vegetation established by the general surveys, but specifically to determine the main communities. Ecological relationships in terms of habitat and biotic relations, and the functional community processes such as plant succession, are investigated in greater detail for the main plant communities. Such surveys may be based upon lists of species from non-defined samples, or on a low density of sample plots within the main community types that are defined by relatively gross physiognomic, floristic and ecological criteria. Mapping scales are from 1: 1 000 000 to 1: 50 000. Appropriate air photo scales for visual photo interpretation in such surveys are between 1: 40 000 and 1: 500 000, obtained from fairly high altitude and wide angle air photography. At the smaller scale, stereoscopic cover is not necessary, but at the larger scales it becomes desirable to assist in more detailed interpretation.

The photographic products of small scale vary from sophisticated satellite-borne media, such as multi-spectral imagery and radiometric methods, to infra-red false colour for high-level photography (scale 1: 150 000). The only larger scale photo products, which have until recently been available, are panchromatic film or infra-red colour photography. Colour photography is not usually recommended due to the problem of haze penetration making colour photography impractical.

In areas where cloud cover is virtually continuous and atmospheric moisture level is extremely high, as in Nicaragua (Crook & Kyle, 1972) and Panama (Crandall, 1969) in Central America, radar has been used as a remote sensing device which can penetrate cloud to give imagery for this scale of survey.

Use of computer classification procedures of feature extraction on digital imagery at this scale of operation is ideal. Compressing the spectral information to a 10 × 10 pixel matrix, with each unit used in the subsequent processing being 44,0 ha in extent, results in a line printer map product which is approximately 1: 250 000 in scale. This is an ideal scale for operation due to the availability to all potential users of 1: 250 000 Topographic and Topocadastral series produced by Trigonometrical Survey for the whole of South Africa.

Jarman, Bossi & Moll (1981) found that the reconnaissance scale of operation best utilizes the digital satellite data, as the classification routines involved compress the spectral information into manageable proportions. The returns on time and the amount of field control work necessary to produce a satisfactory classification are good.

The final map product of this scale of survey is between 1: 1 000 000 and 1: 50 000, whereas remote sensing products would be at scales of 1: 500 000 to 1: 40 000. This would require a reduction in scale of between 10 and 2,5 times from the remote sensing image to the map.

The classification of vegetation used here remains general with divisions on gross criteria such as major physiognomic formations being recognized, together with qualifying floristic data in terms of major dominance types. This type of mapping has been used extensively in areas where basic resource surveys of developing countries were required to enable initial apportionment of an area for efficient land utilization.

The field information required to produce maps of this type is based on a low density of actual samples. This means that communities recognized have a type situation where some method of vegetation analysis was applied and a number of these type situations were grouped to give a vegetation classification. The community type is then associated with its aerial photo image and, often, a site type, and an overall picture is obtained of the vegetation by annotating recognizable vegetative communities. This scale of survey is carried out by the Directorate of Overseas Surveys, United Kingdom (Aitchison *et al.*, 1972), with vegetation communities such as *Acacia raddiana* tree and shrub savanna, *Boswellia* Woodland/Tree savanna, being recognized.

This scale of survey has not been much used in South Africa, possibly as air photography in South Africa was, until the late 1950's, taken at scales of 1: 20 000 and 1: 30 000 only. Acocks's (1975) vegetation map, although published at a scale of 1: 1 500 000 and therefore grouped as a General or General Reconnaissance Survey, contains detail sufficient to be classed as a Reconnaissance Survey.

4.3 *Semi-detailed surveys*

These have the objective of discerning, defining and investigating vegetation upon the basis of the plant community. The physiognomic and floristic structure of the community and its habitat are determined by analysing circumscribed sample plots. Mapping of the plant communities is at scales from 1: 10 000 to 1: 50 000. This corresponds approximately to the medium scale of the Directorate of Overseas Surveys, which recognizes scales from 1: 25 000 to 1: 125 000 as the medium scale limits, but with an emphasis on 1: 50 000 (Read *et al.*, 1973). These surveys are of major importance in defining, classifying and studying community and habitat relations from quantitative or semi-quantitative data. They provide also the main classificatory reference framework for ecosystems from which the extrapolations and predictions provided by more detailed studies can be made. They are the type of survey upon which most management procedures of an area are based. Appropriate air photo scales for such surveys are from 1: 5 000 to 1: 20 000, for upon these air photograph scales can be determined the various plant communities, and measurement of vegetation density and cover can be made with reasonable accuracy appropriate to the scale of survey. However, where such photo scales are not available, use can be made of 1: 30 000 to 1: 40 000 scale photos for devising appropriate sampling strategies and tactics, as well as for the final mapping of the vegetation.

The main remote sensing product used in the past was panchromatic prints. This level of survey is, however, ideally suited to colour photography.

The emphasis in this scale of survey is on a moderately high plot sample density which records vegetation pattern at an Association level (Shimwell, 1971), and air photos are important in all phases. As they are especially important in the field, positive transparencies are impractical.

Stereoscopic coverage is essential at this level of survey to increase accuracy of visual interpretation and, thereby, use of the imagery to its maximum advantage.

There are a number of classification methods which may be used to group vegetation into classes at this scale. The methods most commonly used are physiognomic and dominance type ones similar to the previous survey scale, but the pattern of vegetation recognized is finer. Floristic methods too, such as those of the Braun-Blanquet approach, may be applied effectively to classify the vegetation. Computer classification techniques applied to Landsat digital imagery can be utilized at this scale of operation, but must be based on good ground truth and precise location of samples using ground control points. One of the benefits of digital Landsat imagery is its versatility when it comes to scale of operation. It can be used from a map scale of 1: 20 000 to 1: 250 000, and the units of resolution can be adjusted to meet the requirements of each scale of operation. At a semi-detailed level of investigation single pixels are used as classification units (Jarman & Jackson, 1981). These techniques were applied with some success at a semi-detailed level of investigation in the Langebaan area (Jarman & Jackson, 1981). In this study, the map units defined were structural units and not floristic ones.

Computer classification of digitized standard air photo products would be more appropriate to this level of survey, since the floristic differences which are not readily discernible from satellite imagery become so on air photo products of 1: 20 000 and larger.

4.4 *Detailed surveys*

These have the purpose of studying in detail the structure and functioning of one or more of a group of closely related plant communities (or ecosystems). Such surveys are based on intensive quantitative sampling of vegetation and environment and mapping is at scales larger than 1: 10 000. The results of these surveys can be extrapolated and predicted on the basis of the classificatory reference framework provided by the semi-detailed and coarser surveys.

Air photograph scales that are used must be larger than 1: 5 000 so as to allow species of trees and large shrubs to be recognized, measurements of heights, density and cover of the strata plants to be made, and large scale mapping to be done.

This scale of survey provides the largest range of possibilities for using remote sensing techniques. Standard panchromatic and colour prints may be used for a synoptic view, fieldwork, and orientation with a particular area. For better definition, positive transparencies, especially of the infra-red colour type, may be used. Enhancement of certain features requires multi-spectral photography. Radiometric methods, such as radar, may also be used. These methods provide information in various forms, especially computer compatible tapes, but thus far have not often been used.

The scale requirements of the various products are varied and the platforms required to raise the remote sensing instruments vary from aircraft, helicopters, balloons (Rosetti, 1963; Whittlesey, 1970) to booms and ladders (Whittlesey, 1966; Pierce & Eddleman, 1970). In the other survey scales vertical and stereoscopic products of remote sensing are required to give photogrammetrically correct images, but in detailed work some recordings may be made from oblique angles where, although scale is variable and stereoscopy often not possible, the desired detail is obtained (Harris & Honey, 1973).

The object of carrying out detailed surveys is usually not merely to record the position of plant communities, or individual plants, depending on the particular scale, but to study community or individual form and function. There are usually other measurements required and the map is merely to record where and in what state the vegetal components are at a particular time.

Methods of studying and classifying vegetation are often quantitative at this level of investigation, though other methods such as the Braun-Blanquet approach can be used, provided the desired pattern of vegetation is reflected in the communities recognized.

Although computer classification of Landsat data can be carried out at these levels, using single pixels as classificatory units, it is at the limit of resolution for this imagery.

Again, the digitization and classification of air photoproducts would be more appropriate.

4.5 *Ultra-detailed surveys*

These surveys consist of detecting patterns of within plant community species groups, sociability ratings, microhabitat species specificity, and microhabitat structural or functional relationships, phenological studies, linking to ecophysiological approaches, biomass estimates, etc. Remote sensing platforms are essentially groundbased, e.g. tethered balloons, frames, ladders, etc., and ground sampling is intensive and quantitative. Succession can be monitored after fire, and measurements are made directly off the photos. Stereoscopy is helpful for direct measurements off photos. There are techniques for taking vertical pictures from directly above as well as at right angles to the sample site from which measurements can be made (Adams, pers. comm., 1981). Imagery is not used in ultra-detailed studies to the degree that it should be. As a permanent record at a particular time, it cannot be bettered.

5. MONITORING VEGETATION CHANGE

The objectives of vegetation monitoring must be well defined so that appropriate choice of techniques can be made. For instance, it is necessary to know what must be measured and what degree of detail and precision is required: height, cover, density, or productivity of dominant or certain species, growth form, community or regional changes, or small sample plot changes. The regularity of recording and imagery to meet these requirements must be ascertained, i.e. when and how often should measurements be made? Finally, careful consideration must be given to what ground observation requirements for calibration and verification are necessary in order to make the appropriate choice of remote sensing product and interpretation technique.

Once the objectives have been defined, the appropriate scale of operation can be selected and the appropriate remote sensing product motivated for. Monitoring something like normal regional habit change would require, for example, Landsat imagery taken at yearly intervals. Monitoring incidence of and extent of fires on a regional basis would require at the minimum seasonal coverage, and preferably coverage as regularly as it becomes available during the fire season. At the theoretical best this is once every eighteen days for Landsat imagery.

At the scales for which processing of digital Landsat data is best suited (1: 50 000 to 1: 250 000), provided the various programme parameters are kept constant and cloud cover percentage controlled, once a scene has been processed for one date, change can readily be detected on subsequent dates. It is not necessary to define what the change is in terms of precise detail, but to identify where it is for field checking. Work done in the Langebaan area has shown the strong link between plant community height, canopy cover, type of substrate and spectral map class (Jarman, 1981). Incidence of normal successional changes in plant communities will not be easy to detect, but the incidence of dramatic changes in canopy cover and height of dominant strata due to accelerated erosion, fire, brush-cutting, clearing of areas for development, etc., will be readily monitored.

6. AVAILABILITY OF IMAGERY

The importance of this cannot be sufficiently stressed. In South Africa, imagery available to all users not requiring special motivation is the standard black and white panchromatic product produced by Trigonometrical Survey. For its own purpose of mapping the country at a scale of 1: 500 000, the office of the Director General of Surveys plans to cover the Republic with panchromatic photography at a contact print scale of 1: 50 000 in approximately ten year cycles. The first cycle was initiated in 1971. They are currently also conducting experiments with 1: 150 000 photography for the purpose of monitoring changes. Depending upon the nature and scale of changes detected, it will be decided whether or not additional second cycle photography at 1: 50 000 is required. This means that areas subject to rapid development will probably be re-flown at 1: 50 000 earlier than static areas, and ultimately of course, more often.

Other photography is organized and supervised by the Director General of Surveys on the following basis:

1. Areas for which orthophoto mapping has been requested and approved are flown at 1: 30 000 specifically for the production of the orthophoto maps, at a scale of 1: 10 000;
2. Black and white photography requested by other Departments, such as the Department of Agriculture, is normally flown at a scale of 1: 30 000 or 1: 40 000;
3. Special jobs at other than the scales mentioned above and including colour photography are considered individually and treated according to merit.

The whole air survey programme, including both photography required for the Director General of Survey's own mapping work and that requested by other Departments, is considered by the National Advisory Survey Committee. The size and content of the programme approved by the committee depend largely upon available funds, and the motivations submitted by other departments.

As can be seen from the foregoing, it is most unlikely that the major established conservation areas will be included in areas flown on a *routine basis*, because by their nature they are areas of zero, or very limited, development or change. The scale of routine photography (1: 50 000 or 1: 150 000) has so far been of relatively limited value for interpretation and mapping of vegetation and even for transfer to base maps at 1: 50 000 (Bands, 1978).

The availability of Landsat imagery, prior to direct reception by Hartebeesthoek Satellite Remote Sensing Centre was sporadic. Within the study carried out on Fynbos Biome mapping, of the 15 Landsat images needed to cover the whole Fynbos Biome geographic area only 12 were available for the whole of the 1972/73 period. (Bossi, pers. comm., 1981). It was not possible to investigate either monitoring of habitat change or effects of season on vegetation mapping from the available imagery in the investigation carried out by Jarman, Bossi & Moll (1981). Even with direct, regular reception, availability of imagery remains a problem. Cloud cover is a problem, especially along coastal and mountainous areas. Fraser & Curran (1976) report on two hypothetical satellite survey missions in which the success of the first mission requires at least one observation of the entire 185 km^2 field of view without cloud, and the second permits viewing whatever cloud free areas exist. On successive satellite passes new cloud free areas may appear, and a mosaic of the field of view can thus be assembled. The result of this theoretical exercise showed that the entire field of view could be seen on mosaicing with high confidence after 7 satellite passes, whereas the entire field of view could be seen with only 50% probability after the same number of passes. For a 90% probability of success 22 passes were needed. This emphasizes the importance for informed national integrated planning when motivating for adequacy of scale of product and regularity of recording of imagery to be used in vegetation monitoring and seasonal studies.

7. MAP PRODUCTION

It is not intended to deal in any detail with the variety of photogrammetric instruments and approaches to cartography available to vegetation mappers. It suffices to say that the development of map categories, consistent identification of photo units in visual interpretation, and subsequent transfer of information on to a map presents the biggest obstacle to most workers. More often than not, maps are not produced.

At the larger scales in semi-detailed work, tying large scale air photo products to digital processing at the map production stage is, therefore, a very practical solution. It is also suggested that establishing contact with photogrammetric and cartographic units with professional assistance at this stage saves time and money in the long run. Computer classification of digital imagery has the advantage that map production is part of processing. Products can be viewed or photographed off TV screens, can be in line printer output form with suitable correction to scale as part of the processing, or can be in photo print form from computer optronics output. Again, the latter can be produced at any desired scale.

8. SYNOPSIS OF AN INTEGRATED APPROACH TO VEGETATION SURVEYING AND MAPPING

The approach to the use of remote sensing products for vegetation mapping can be broken down into three basic steps: data collection, interpretation and product generation. Developments in the techniques involved in interpreting imagery have tended to polarise the approaches into either image oriented approaches or numerically oriented approaches. Fig. 1 from Fleming & Hoffer (1977) shows the interrelationships between the image oriented and numerically oriented system and the possible links between the systems.

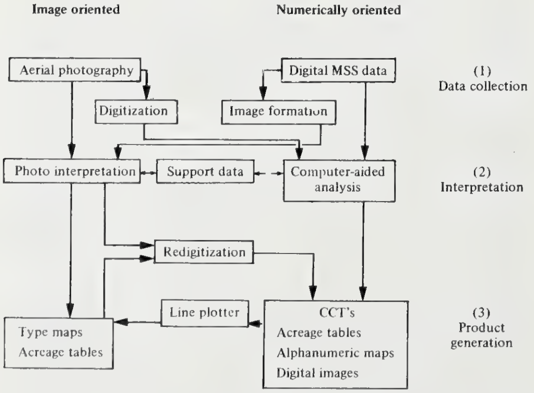

FIG. 1.—Interrelationships between the image oriented and numerically oriented system and the techniques of going from one system to the other (after Fleming & Hoffer, 1977).

Although both approaches utilize data collected from a remote location, the characteristics and format are different. The first step of data collection is covered in Section 3, which describes the products available to vegetation mappers either as aerial photographs and digital products. At the second step different approaches are used. Photo interpretation relies on trained interpreters to do the analysis by identifying and delineating the various vegetation types. Computer aided analysis techniques replace the repetitive steps of identification and recording of decisions with a computer, thus reducing bias and increasing speed (Bauer, 1976).

The third step in both approaches is dependent on the feature extraction process. Product generation for the image oriented approach entails producing a map by transferring boundaries from annotated photo-units onto a base map. Areas of features of interest are measured using dot grid or planimeter techniques.

In the numeric approach, the interpretation is recorded on CCT's as the decisions are made. Alphanumeric maps, digital images and estimates of map class areas are produced by computer algorithms that summarize data from the CCT's.

Fig. 1 shows the interrelationships between the two approaches. Aerial photography can be digitized by a scanning microdensitometer to convert the photographs to a digital format. Conversely, digitized photographic or MSS data can be converted to an image on a TV screen or on photographic film. Once data have been displayed, interactive systems allow for interpretation, redigitization and storage on CCT's. Map products from visual interpretation techniques can be digitized, stored and handled on CCT's (Boyle 1972a & b). The reverse can also be achieved in that digital information can be presented as line type maps on a plotter system.

It is recommended that the best aspects of both approaches be utilized in a fully integrated approach to a mapping problem.

9. CONCLUSIONS

Plants are a measure of the conditions under which they grow and act as an index for soil and climate. The fact that changes in vegetation occur is visible proof of the dynamic nature of the environment. It is necessary to be able to record and follow vegetation changes in order to predict and determine and control any changes which could severely upset the desired balance.

Various scales of surveys are required to provide planners with a complete picture. Small scale surveys at the general and general reconnaissance levels provide pictures of the overall situation and modern satellite imagery can quickly and effectively monitor changes.

Regional surveys provide the information for broad policy determination and planning for areas which have similar problems.

The semi-detailed survey provides for resource management planning even down to the farm level.

Detailed surveys include studies of ecosystems. Knowledge of the structural and functional attributes of ecosystems provides the means whereby appropriate ecosystem management can be devised by the pasture or other applied scientist. The role of vegetation mapping is therefore of major importance.

Remote sensing products are desirable for most surveys at any scale. The advantage of having remote sensing products is that they provide a permanent record of a situation at a particular time. Differences may then be plotted over a number of years if so desired. Certain areas which are inaccessible by normal transport and areas of this nature can best be surveyed using remote sensing techniques. In other areas, although it is possible to work without remote sensing, the rate of progress would be slower and boundaries would be less accurate than those given by the synoptic view. The time and effort saved in fieldwork offsets the additional cost of acquiring imagery.

Remote sensing products are therefore almost essential for survey work. Their use, however, should be restricted to situations where the information required can actually be obtained using this approach.

10. ACKNOWLEDGMENTS

The staff of the Ecology Section, Botanical Research Institute, over a period of years are thanked for stimulating discussion. Financial support from the CSIR National Programme for Environmental Sciences within the Fynbos Biome Project and the CSIR National Programme for Remote Sensing is acknowledged and appreciated.

UITTREKSEL

Effektiewe gebruik van afstandswaarnemingstegnieke vir die kartering en monitering van plantegroei, is 'n funksie van skaal, resolusie, afbeeldingsseisoen, soort plantegroei, sensoriese en spektrale sensitiwiteit, verwerking van die afstandswaarnemingsproduk en spoed en noukeurigheid waarmee inligting oorgedra word op die karteringsproduk.

Die soort van afbeelding, tipe van data en algemene verhoudings tussen skaal van studie, skaal van kartering en skaal van afstandswaarnemingsproduk wat van toepassing is op die Suid-Afrikaanse situasie vir visuele en digitale ontleding, word aangebied. Die tipe van afstandswaarnemingsproduk en verwerking, die toepaslike veldwerk en die doel waartoe kaarte op elke skaal geteken word, word bespreek. Gebrek aan herhaaldelike afbeeldings tot op datum, het nie voorsiening gemaak vir die volledige ondersoek van moniteringspotensiaal nie. Versigtige beplanning op nasionale vlak word benodig om die beskikbaarheid van afbeeldings vir moniteringsdoeleindes te verseker. Kaartproduseringsprosesse wat vinnig en akkuraat is, behoort benut te word. 'n Geïntegreerde benadering tot die opname en kartering van plantegroei wat die beste eienskappe van beide visuele en digitale verwerking insluit, word vir gebruik aanbeveel.

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Montane plant environments in the Fynbos Biome

B. M. CAMPBELL*

ABSTRACT

Environmental data collected at 507 plots on 22 transects, and soil analytical data from 81 of these plots, have been used to describe the plant environments of the mountains in the Fynbos Biome. Two major regional gradients are recognized: a west-east gradient and a coast-interior gradient. Of particular consequence for fynbos-environment studies is the increase in the proportion of fine soil particles from west to east. At least some aspects of soil fertility also increase towards the east. The edaphic changes are paralleled by climatic changes: chiefly a decrease in the severity of summer drought towards the east. On the coast-interior gradient a major non-climatic variable in the gradient is rock cover. High rock cover is a feature of the interior ranges. Soils with organic horizons or with E horizons are a feature on the coastal mountains, but are generally lacking on the interior mountains.

The other environmental gradients recognized occur on individual transects and all include edaphic variables. The rockiness-soil depth gradient, on which an increase in rockiness is associated with a decrease in soil depth and usually a decrease in clay content, tends to occur in three situations. Firstly, it is associated with local topographic variation; the shallow, rocky soils being a feature of the steeper slopes. Secondly, it is associated with the aspect gradient; the hot, dry northern aspects having shallow, rocky, less developed soils. Thirdly, it tends to be associated with the altitude-rainfall gradient; shallower soils being found at higher altitudes. It is also at higher altitudes that higher rainfall is found. Variation in oxidizable carbon is chiefly accounted for by the altitude-rainfall gradient. Whereas at a biome-wide level, aspects of soil fertility are related to soil texture, it appears that on individual transects fertility is linked to amounts of plant remains in the soil and to rainfall.

Apart from these gradients, which are found on the Table Mountain quartzites, other sources of environmental variation are due to the differences between geological types. The non-quartzitic soils are generally deeper and finer-textured. It is suggested that the nutrient-poor/nutrient-rich distinction must be used with care; at least in the mountains the distinction should not automatically be substituted for the quartzitic/non-quartzitic distinction.

INTRODUCTION

In this paper I describe the variation in plant environments that occur in the mountains within the Fynbos Biome. This work provides the setting for the ecological interpretation of vegetation structural-functional features and vegetation types and, as such, is part of the project aiming at a vegetation classification of the mountains of the Biome. The project and the vegetation-environment interactions are described elsewhere (Campbell, in press a, b, c).

In the present account I limit myself to presenting new environmental data, to unravelling the interrelationships among environmental variables, and to identifying the major gradients; I do not attempt to review the already well-reviewed topic of fynbos environments (Lambrechts, 1979; Fuggle & Ashton, 1979; Kruger, 1979a). Fire and factors such as grazing are not dealt with here as the vegetation classification was limited to mature vegetation (cf. Campbell, in press a).

METHODS

The study area

The study area consists of all the mountains in the area delimited as the Cape Floristic Region (Goldblatt, 1978), the boundaries of which correspond roughly with the Fynbos Biome (Kruger, 1979b). Also included are the patches of fynbos mapped by Acocks (1953) that occur outside the Cape Floristic Region (Fig. 1). The vegetation of the study area is mostly Mountain Fynbos (*sensu* Taylor, 1978) but also includes forest, grassland and dry non-fynbos shrublands (e.g. Valley Bushveld, Succulent Mountain Scrub, Karroid Broken Veld — Acocks, 1953).

Data recorded

Environmental data have been collected from 507 plots located on 22 transects in the study area (Fig. 1). Each transect spans a mountain. Details of transect and plot location are in Campbell (in press, a, c.). Although plot selection was not random, I have used the plots to describe environmental variation in the study area, and have noted in the text the obvious biases (e.g. precipitous cliffs have not been sampled).

In each plot, 17 easily measured or estimated environmental variables were recorded. For each transect, 3 climatic variables were recorded using the data of Fuggle (1981) which come from climatic stations at or near the base of the transects. The environmental variables collected are summarized in Table 1.

In addition, soil samples were taken from 81 plots. The most detailed soil sampling was done on the Cedarberg transect (29 plots), so as to complement the data becoming available for other regions of the study area (Bond, 1981; Cowling, 1983; Kruger 1974, 1979a; Low, in prep.). The remaining soil samples were located throughout the study area. They have been especially used to check the field estimations of texture, and the field assignment of soils to soil types. The soil samples analysed here were collected from depths of 20–30 cm, except where soils were shallower. The variables assessed and the methods used in the soil analysis are shown in Table 2.

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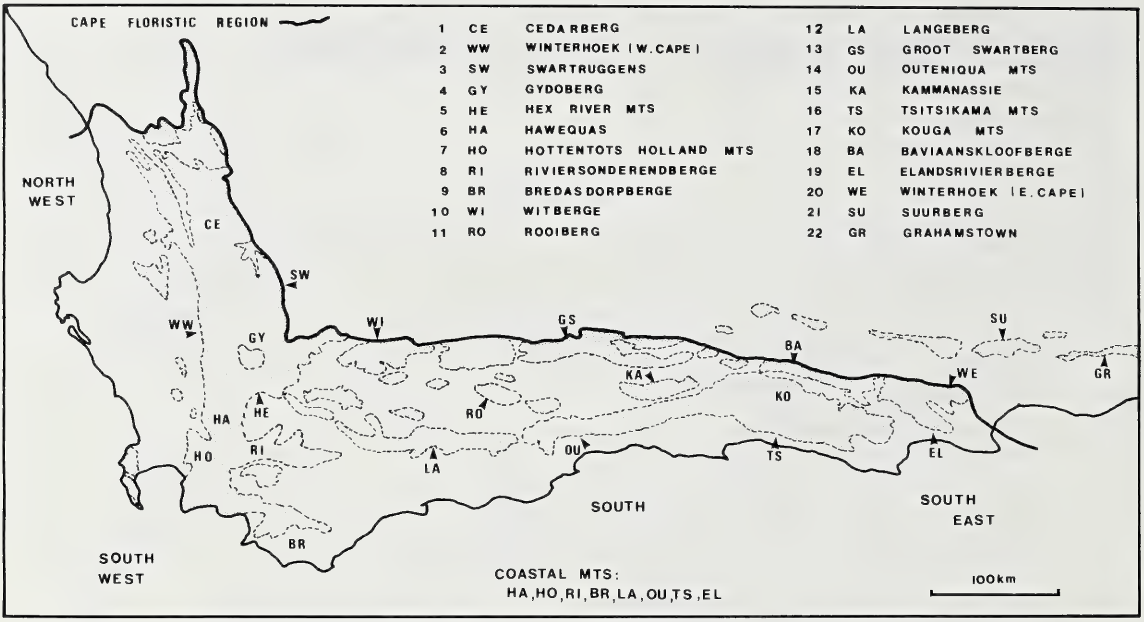

FIG. 1.—The study area and the study transects. Shading indicates fynbos of the mountains (after Acocks, 1953). Transect numbers and abbreviations are given, and the geographical regions referred to in the text are shown.

TABLE 1. — The environmental variables recorded. The abbrevations used in the text and the methods and/or classes used are shown

Abbreviation	Environmental variable recorded in each plot
ALT	ALTITUDE 1:50 000 topographic map.
RAI	ANNUAL RAINFALL 1:250 000 isohyet maps. These maps are not very accurate and many of the patterns represent cartographic interpolation (Fuggle, 1981).
GÉO	GEOLOGY Geological maps of various scales.
ASP	ASPECT 1=NE 2=N; 3=E; 4=NW; 5=W; 6=SE; 7=S; 8=SW: a hot to cool gradient (c.f. Whittaker, 1960).
TER	TERRAIN MORPHOLOGICAL UNIT MacVicar *et al.*, 1977: 1=crest; 2=scarp; 3=middleslope; 4=footslope; 5=valley bottom.
TOP	TOPOGRAPHY/DRAINAGE UNIT 1=open slope; 2=protected canyon position; 3=seasonal standing water; 4=seasonal seepage on open slopes; 5=seasonal stream; 6=perennial stream.
SLO	SLOPE INCLINATION
CLA	% CLAY CONTENT Estimated clay content of A horizon (U.S. Dept of Agric., 1951).
TEX	SOIL TEXTURE Estimated soil texture of each horizon (U.S. Dept of Agric., 1951).
SOI	SOIL TYPE Macvicar *et al.*, 1977.
DEP	SOIL DEPTH
RO1..RO5, ROT	ROCK COVER (%) BY ROCK SIZE CLASS RO1=rocks with less than 5 cm diameter; R02=5 −50 cm; R03=50−150 cm; R04=greater than 150 cm; R05=bedrock; ROT=total rock cover.
FOR EACH	TRANSECT
EVA	ANNUAL PAN EVAPORATION
TEM	TEMPERATURE RANGE Summer (3 months) mean daily temperature minus winter mean daily temperature (Fuggle, 1981).
WIN	% WINTER RAINFALL Percentage of rain that falls in the 3 winter months (Fuggle, 1981).
NUM	TRANSECT NUMBER Transects are numbered 1 to 22 from the north to the south east (Fig. 1).

Data analysis

To understand the relationships between environmental variables, I have mainly used correlation coefficients. Many relationships are discussed by reference to the correlation matrix of Table 4, which was calculated for the 354 plots of the open slopes (TOP=1)* of the Table Mountain Group. To answer the question whether relationships are similar on each transect, correlation matrices were calculated for each transect, and the correlation coefficients between specified variables were then combined to give a single assessment of the relationship (Table 5). For instance, correlation coefficients between altitude and rainfall for 19 transects are combined to give a single assessment of the trends on all transects. The method of combination is that of Fisher (1970). It combines the p-values corresponding to the correlation coefficients to give a single χ^2 value with d.f. = (n=19) × 2. Poorly sampled transects were excluded from this analysis (GR, BR, KO excluded; cf. Campbell, in press c; therefore n = 19 transects). I use 'combined χ^2' to differentiate the above from other χ^2 tests. The strengths of the relationships between variables as indicated by the above results are reported in the text by using the symbols of Tables 4 & 5 (e.g. +++ and ***). These symbols are given to test statistics with at least $p<0,005$, and throughout this paper one-sided p-values have been used when appropriate.

I have used principal components analysis (PCA) to summarize correlation matrices. The more easily interpreted rotated factors are reported here (varimax rotation; Morrison, 1976).

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*Abbreviations of variables as in Table 1 and abbreviations of transects as in Fig. 1.

TABLE 2.—Soil variables assesed in 81 plots. The abbreviations used in the text and the methods used are shown

Abb.	Soil variable		Method
CL	Clay %		Pipette method (textural classes according to MacVicar *et al.*, 1977)
SI	Silt %		
FS	Fine Sand %		
MS	Medium Sand %		
CS	Coarse Sand %		
	Sodium	Exchangeable cations	1N NH, acetate leachate
	Potassium		
	Calcium		
	Magnesium		
S	S value		Sum of exchangeable cations
N	Total Nitrogen		Kjeldahl
P	Available Phosphorus		Bray No. 2
C	Oxidisable Carbon		Walkley-Black method
pH	pH		1 N KCI 1:2,5 soln
	Colour		Munsell colour chart
	Stoniness		% by weight of stones > 2 mm

Although plot selection is non-random, I do use statistical methods to explore the data matrices and to describe the strengths of relationships between variables, if only as a labour-saving and page-saving device. The quoted statistical results from Table 4 & 5 would be considered very highly significant in a statistical study; here they must be seen as indicating possible degrees of relationships.

PHYSIOGRAPHY

Geology

The landscape of the Fynbos Biome is dominated by the mountains of the Cape Folded Belt, which consist mainly of hard quartzitic rocks belonging to the Table Mountain (T.M.) Group and Witteberg Group. Of the several mountain chains only the minor interior ranges are of the latter geological type (represented in the sample by transects GY, SW, WI, SU, GR—Fig. 1). Shales, phyllites, slates, conglomerates and granites are mostly restricted to the intermontane valleys (out of the study area) and lower mountain slopes; exceptions to this being the relatively numerous narrow bands of shale in the Witteberg Group and the single high-altitude shaleband (Cedarberg Formation) in the T. M. Group. Table 3 shows the relative abundance of the various geological types encountered in the present study (see Lambrechts, 1979, for a geological map of the Fynbos Biome, and further discussion).

Topographic analysis

Altitudes recorded in the present study (Fig. 2) indicate that average altitudes are generally higher in the interior ranges of the south and in the west (see also Table 4). Maximum altitudes are in the order of 2 000 m.

Slope inclinations recorded range from 0° to over 40° (Fig. 3.) Gentle slopes (≤4°) are significantly associated with transects of the north west (χ^2 = 30,1, d.f. = 16, $P<0{,}025$; CE, HE, SW, WW all contributing large values to the χ^2). It is in this

TABLE 3.—Geological types included in the sample. The distribution of plots among geological types gives an indication of the relative abundance of a geological type

Geology	No. of plots	Where sampled
Tertiary to Quaternary		
Alluvium	9	Valleys
Silcrete	4	Plateaux at base of lower slopes (east)
Uitenhage Group (Enon conglomerate)	7	Lower slopes (east
Karoo sequence (Dwyka shale)	2	Lower slopes
Witteberg Group		
Shale, siltstone	2	Interior mountain ranges
Sandstone, quartzite	62	
Bokkeveld Group		
Shale, siltstone	3	Lower slopes
Sandstone	2	
Table Mountain Group		
Quartzite	374	Coastal and interior mountain ranges
Shale	26	High-altitude shaleband
Malmesbury Supergroup (shale)	4	Lower slopes
Cape Granite	12	Lower slopes (west)

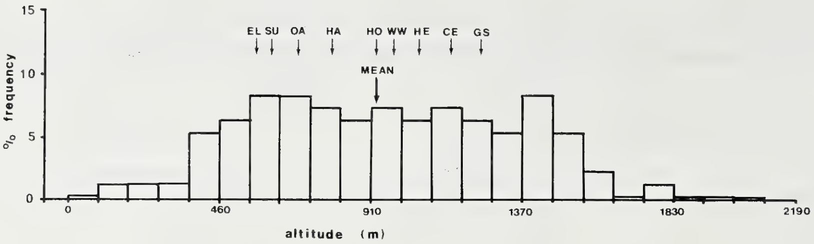

FIG. 2.—Frequency of altitude classes and mean altitude from various transects. For this frequency distribution and those to follow, n = 507 (except in cases of a few missing data values).

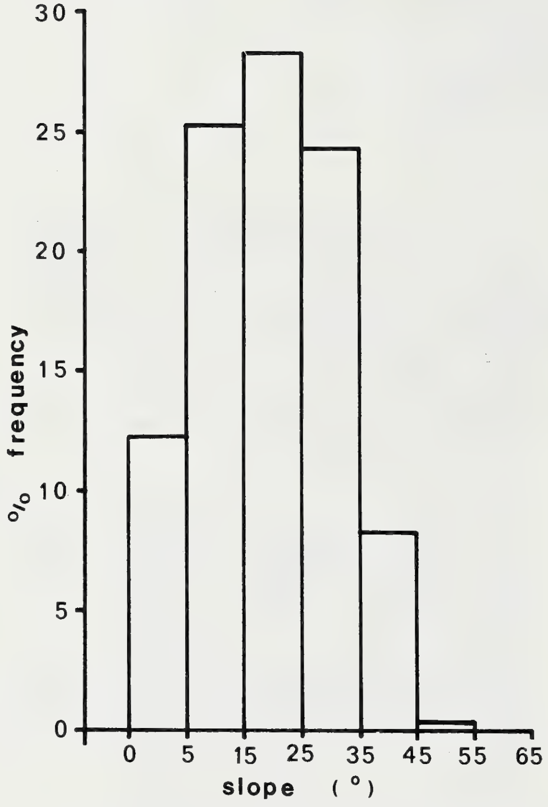

FIG. 3. —Frequency of slope inclination classes. A systematic sample of slope inclinations from 200 points in a small south-western catchment shows a very similar pattern (Kruger, 1974).

region that one gets extensive summit and subsummit plateaux; they are usually lacking elsewhere. The steepest slopes recorded ($\geqslant 35°$) are associated with the more coastal, southern ranges ($\chi^2 = 23{,}8$, d.f. = 16, $p < 0{,}1$; KO, TS, OU, KA all contributing large values to the χ^2). This last association is not the true situation, for my sample reflects vegetated slopes, and does not include precipitous cliffs. It is in the western zone that extremely steep cliffs are found, often with little or no vegetation (e.g. with 60–80% surface rock cover in areas; F. Ellis, pers. comm). Ellis (pers, comm.) records mean slopes of 30° to 42° in the Hex River Mountains whereas my mean slopes for the western area are 15° to 18°. The many steep slopes indicate the considerable relief of the study area. Differences in altitude of 1 000 m in distances of 3 km are not uncommon.

If there is any relationship between slope and altitude, and between slope and aspect, then it is very weak (combined $\chi^2 < 64{,}1$ in both cases). The altitude/slope/aspect relationships are extremely complex owing to the broken landscape. The relationships are not monotonic on a single transect and they differ from transect to transect. For instance (1) in the west the steeper upper slopes are often broken by subsummit plateaux, and (2) some mountains have steeper south aspects (e.g. RI), whereas other have steeper north aspects (e.g. BA). The combined χ^2 values indicate a slight tendency towards steeper slopes at higher altitudes and on south aspects.

Rockiness

Total rock cover is exceedingly high in the study area (49% mean cover, Fig. 4a). Even if the smaller stones are excluded (< 5 cm diameter) the mean rock cover is high (37%). In the soil samples, stones of less than 5 cm diameter average 31% of a sample (by weight) (n = 52, range 0%–75%).

There is increasing rock cover from coastal to interior ranges (++). Mean rock cover per transect is lowest (40%) on coastal mountains, especially in the south and south east. Most rock is either small (<50 cm in diameter – R01, R02) or is bedrock (R05) (Fig. 4b). The cover or rock within a size class is strongly correlated with total rock cover (*** or **, +++) except in the case of large boulders (over 150 cm diameter – R04) where correlation is weaker (*, +). For each rock size class, rock cover is generally higher in the interior and/or in the west (+'s). High cover (>30%) of large boulders (R04) is more or less restricted to the west whereas high cover (>60%) of bedrock (R05) is a feature of the north west ($\chi^2 = 4{,}69$, d.f. = 1,$p < 0{,}025$ and $\chi^2 = 22{,}3$, d.f. = 13,$p = < 0{,}05$ respectively). Variation in cover of small rocks (R01, R02) tends to be more associated with the coast-interior gradient than the west-east gradient (Table 4).

The sampling is of course biased towards vegetated surfaces. The west-east gradient would be more pronounced if this bias was removed. Ellis (pers. comm.) records mean rock cover values of up to 80% in parts of the Hex River Mountains (though his figures are probably not directly comparable. His figures are based on estimates of large areas, whereas mine are estimates of 10 × 5 m plots).

The correlation coefficients for all plots indicate that total rock cover, bedrock (R05) cover, and

TABLE 4.—Correlation coefficients between the environmental variables collected in each plot. Only plots from open slopes (TOP = 1) and the Table Mountain Group have been included (n = 354 plots). Abbreviations of variables as in Table 1. The symbols indicate strengths of positive and negative correlations. As explained in the text, evaporation (EVA) and temperature range (TEM) decrease from west to east but especially from interior to coast, thus other variables correlated with TEM and EVA tend to show similar geographical patterns. If these other variables are strongly correlated with % winter rainfall (WIN) and transect number (NUM), then their geographical variation is essentially west to east; if uncorrelated with WIN and NUM then their variation is essentially interior to coast

	ALT	RAI	ASP	SLO	DEP	CLA	RO1	R02	R03	R04	R05	ROT	EVA	WIN	TEM
RAI	++														
ASP															
SLO	+														
DEP	-		+	--											
CLA	-	-	+												
R01					-										
R02			-	+	--		+								
R03	+			++	-	-	-	+							
R04									++						
R05	+		-	+	---	--	-								
ROT	+		--	++	---	--	+++	+++	+++	+	+++				
EVA	+++					--	+	+	+		+	+++			
WIN	+	+++				---		-		+	+		+		
TEM	+++					--	+	+			+	++	+++	+	
NUM	--	---				+++		+		-	-		--	---	-

- or + /r/ >0, 14 (p <0,005)
-- or ++ /r/ >0,25
--- or +++ /r/ >0,35

TABLE 5.—χ^2 values between selected environmental variables. The χ^2 value combines the correlation coefficients calculated for 19 transects and thus indicates whether the same trend tends to occur on all transects. The directions of the correlations are the same as in Table 4. In the text these χ^2 values are termed 'combined χ^2'

	ALT	ASP	SLO	DEP	ROT
RAI	***				
SLO	n	n			
DEP	*	*	**		
ROT	n	*	**	***	
RO1	n	n	n	*	**
RO2	n	*	*	**	***
RO3	n	n	**	*	**
RO4	n	n	n	n	*
RO5	*	n	*	***	***
CLA	*	*	n	*	*

n $\chi^2 < 64,1$
* $\chi^2 > 64,1$ ($p < 0,005$)
** $\chi^2 > 100$
*** $\chi^2 > 150$

cover of R03 increase with altitude (+'s), but this reflects the association of rock cover and altitude with continentality rather than a rock cover-altitude relationship within individual transects. On transects it is only bedrock which appears to increase with altitude (*). Steeper slopes have higher rock cover (++,**) and more northerly aspects tend to have higher rock cover : (-,*). Ellis (pers. comm.) reports values of 60–80% cover on north aspects in the Hex River Mountains and 40–60% on the south aspects. Bond (1981) working in the Swartberg and Outeniqua Mountains also records north aspects as being rockier.

CLIMATE

Climatic variation in the Fynbos Biome has been recently reviewed by Kruger (1979a), Fuggle (1981) and Fuggle & Ashton (1979). I have not collected original data and I limit myself to summarizing these reviews in a gradient framework. The dissected topography of the biome makes for complex climate patterns. However, the variability can be summarized by reference to 4 gradients: west-east gradient; coast-interior gradient; altitude gradient and gradient from south to north aspects.

The west to east gradient shows the following trends: (1) a marked summer gradient in receipt of solar radiation (30 to 25 MJ m^{-2} day^{-1} from west to east); (2) greater seasonal temperature ranges in the west; (3) higher annual pan evaporation in the west (1800–2000 mm vs 1300–1700 mm) with greater amounts being evaporated during summer in the west (40% vs 35% in the summer 3 months); (4) a pronounced winter rainfall régime in the west (80% vs 35% rain in the winter 3 months) and (5) higher annual rainfall in the west (over 2500 mm on the high peaks of the south west). The climates of the lower mountain slopes of the west are generally mediterranean (Cs — Köppen system) while those of the east are 'steppe' climates (Bsk) or warm temperate all-year rainfall (Cfb) (Fig. 5). Although it is the west which has marked summer droughts, even the Cfb climate has the dry season in summer as it is then that moisture deficits occur (Bond 1980a, 1981). The west-east gradient is not strictly monotonic with respect to a summer moisture deficit, for it is the southern coastal mountains which have the least moisture deficits, with greater deficits to the west and, to a lesser extent, to the east (e.g. Specht & Moll, 1982).

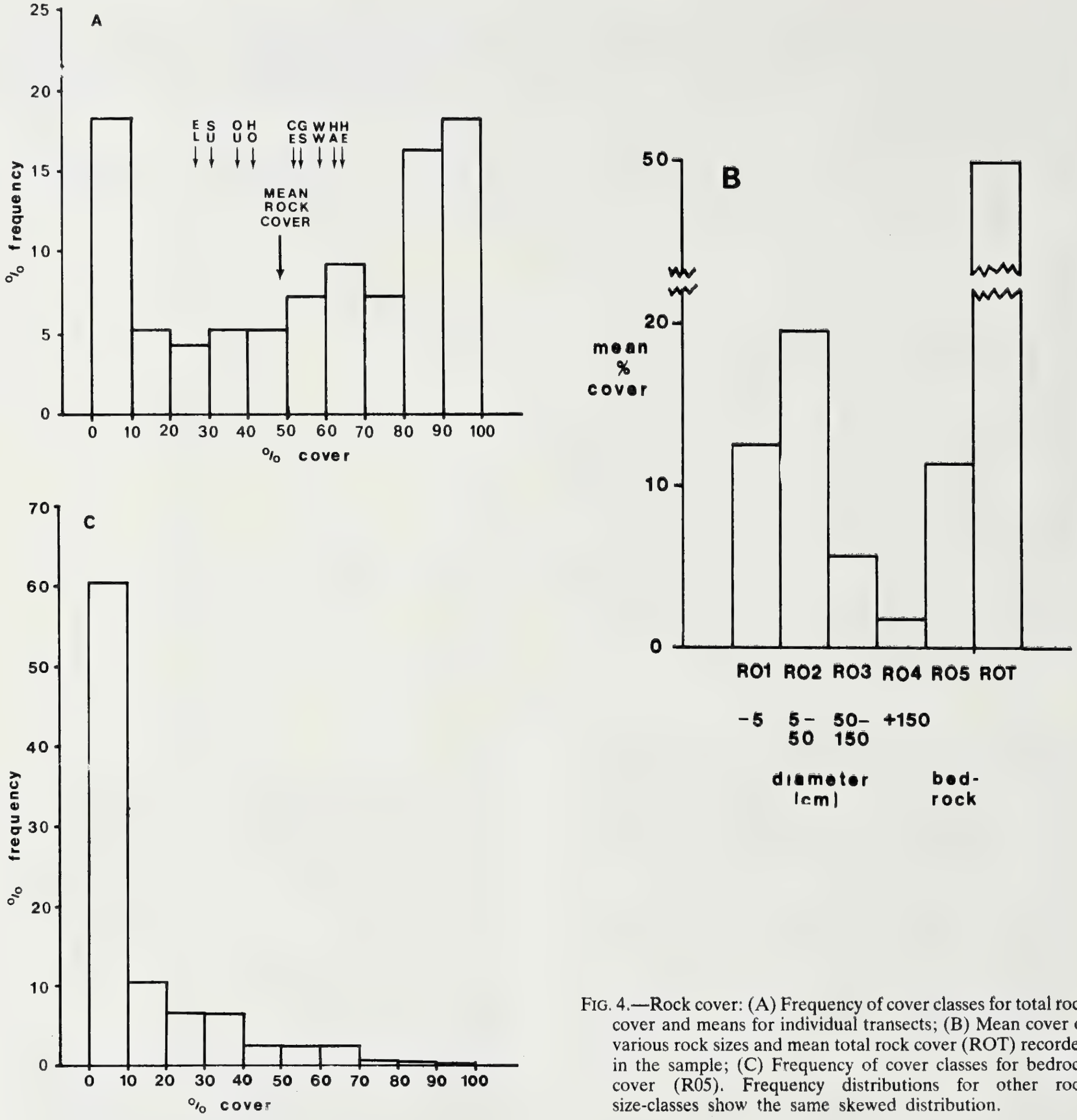

FIG. 4.—Rock cover: (A) Frequency of cover classes for total rock cover and means for individual transects; (B) Mean cover of various rock sizes and mean total rock cover (ROT) recorded in the sample; (C) Frequency of cover classes for bedrock cover (R05). Frequency distributions for other rock size-classes show the same skewed distribution.

Along the coast to interior gradient the following trends can be recognized. On the lower slopes of the coastal mountains there are lower annual temperatures (15°–16°C vs 17°–18°C), smaller seasonal and daily temperature ranges, greater cloudiness, lower pan evaporation (1800 mm vs 2000 mm in the west, 1400 mm vs 2000 mm in the south, and 1300 mm vs 1700 mm in the south-east), and higher rainfall. Considerable summer mists do much to alleviate the summer drought on the high peaks of the coast (e.g. Nagel, 1962). The peaks of the south and south-east coastal ranges, generally lower in altitude, are less prone to snowfall than those of other regions (Bond, 1981; 5,4 snowfalls per annum on average in the study area — Schultz & McGee, 1978). The lowland climates in the west change from cool mediterranean (Csb) at the coast to warm mediterranean (Csa) and eventually in the most interior areas, to 'steppe' and desert climates (Bsk, Bsh). A similar sequence is the rule in the east except that the mediterranean types are not found; they are replaced in the sequence by the all-year rainfall type (Cfb) (Fig. 5).

The altitude gradient tends to have the following characteristics. With increasing altitude, mean annual temperatures decrease (15°–16° to 12°–13° in the south-west), pan evaporation decreases (1800 mm to 1310 mm in the south-west; Kruger, 1974), rainfall increases (from often less than 400 mm to over 1000 mm in the south and to over 2500 mm in the south-west), precipitation from mist increases especially on the coastal ranges, and the likelihood of snow increases. In the south-west there is a change from a Csb climate in the lowlands to a climate which tends to lack a summer drought (Cfb) on the upper peaks (Kruger, 1974; Boucher, 1978). In the more interior ranges, there is a change from a 'steppe' or desert climate in the lowlands to a Cs climate on the upper peaks (Fig. 5).

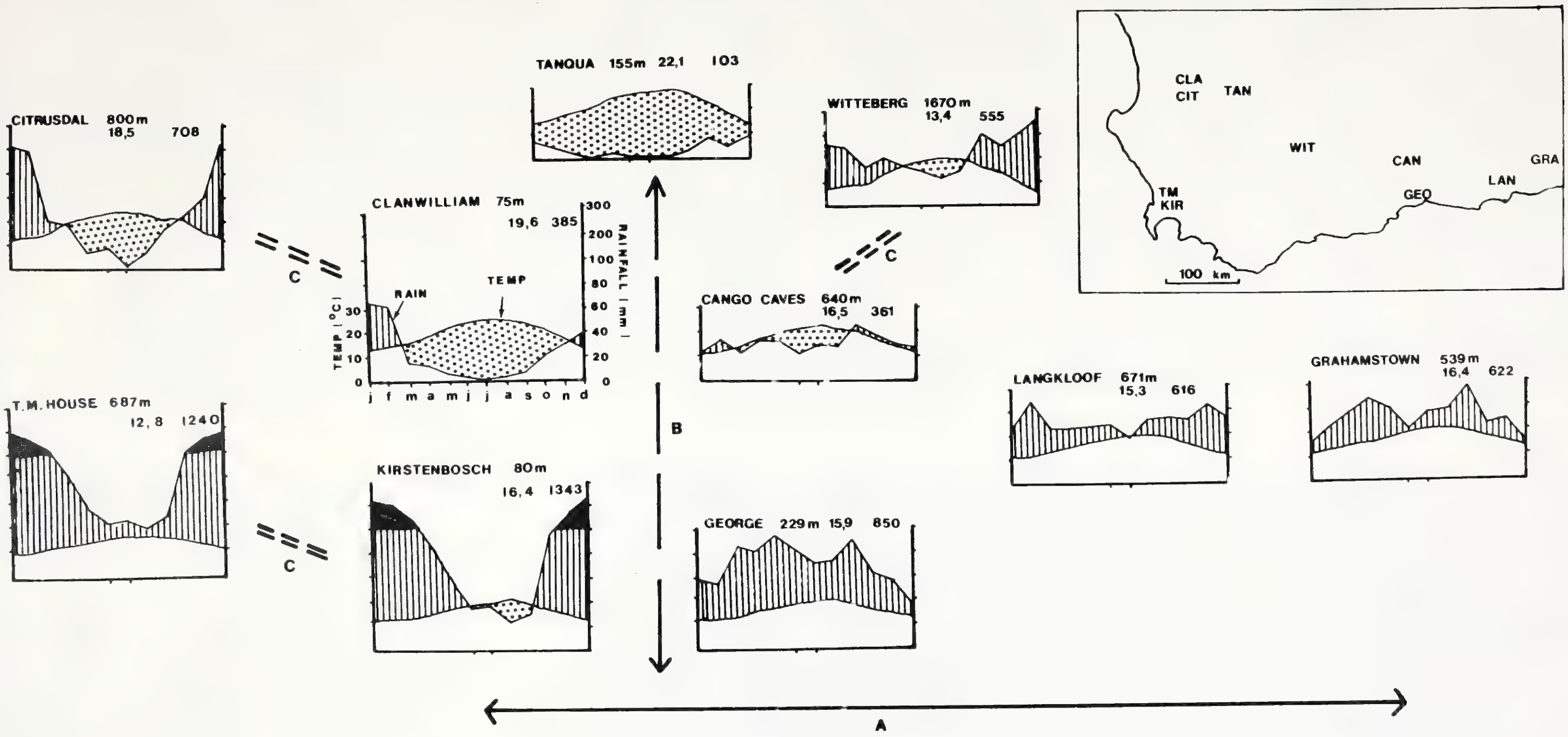

FIG. 5.—Walter-Lieth diagrams for contrasting stations near or in the study area. A, west to east; B, coast to interior; C, low to high altitude. On each climatic diagram the altitude (m) of the climatic station, the mean annual temperature (°C) and the mean annual rainfall (mm) are indicated. The axes are illustrated on the Clanwilliam diagram. The inset indicates the geographical position of climatic stations.

Finally, the fourth gradient is the aspect gradient. There are pronounced differences in receipt of solar radiation between north and south aspects especially in winter. For instance, north aspects of 20° slope receive 4 to 5 times as much energy as the equivalent south aspects during mid-winter. This figure is relevant to the present work, as the average slope recorded is 18°. At least in the southern area, the slopes north of the watershed (generally north aspects) receive less rainfall and less orographic cloud than the slopes south of the watershed (generally south aspects) (Bond 1980b, 1981). Taylor & Van der Meulen (1981) quote 1 year's data showing 50% lower rainfall on the north side of the Rooiberg than on the south side.

In my data set, I have included the following climatic variables: percentage winter rainfall (WIN), pan evaporation (EVA), seasonal range in temperature (TEM) and rainfall (RAI). Transect number (NUM), running from west to east and WIN are strongly correlated (- - -) and are surrogates for the west-east complex gradient. EVA and TEM are strongly correlated (+++) and are surrogates for the continentality gradient. However, they are also correlated to a lesser extent with WIN and NUM (Table 4), and thus the west-east and continentality gradients are not entirely independant. RAI and altitude represent the altitude complex gradient and are highly correlated on individual transects (***). Of the 4 transects which show the weakest altitude-rainfall correlation, 2 were poorly sampled (WI, SU) and 2 were from the southern coastal mountains (OU, TS). In this latter area, there is a strong gradient of rainfall from the coastal slopes to the interior slopes, and therefore the altitude-rainfall relationship is weaker. Altitude and rainfall are also correlated with the regional climatic gradients; higher altitudes tending to be associated with the interior ranges (correlated with EVA and TEM) and higher rainfall being found in the south west (correlated with WIN and NUM—Table 4).

SOILS

Soil depth

Soils in the study area are shallow, a mean depth of 0,5 m being recorded. Only 17% of the recorded depths are over 1 m (Fig. 8) and these are significantly associated with certain geological types especially granite and alluvium and perhaps Malmesbury shales and silcrete (χ^2 = 54,1, d.f. = 10 p<0, 001). Soil depth is highly negatively correlated with total rock cover (- - -,***) and cover of various rock sizes (Tables 4, 5). It therefore shows relationships similar to those shown by rock cover; the shallower (and more rocky) soils being found on steep slopes (- -,**), on the more northerly aspects (+,*) and at higher altitudes (-,*).

Soil texture

In the T. M. Group the strongest relationship shown by percentage clay is the increase in clay content from west to east (+++). The other relationships shown by clay are a decrease in clay content on very rocky sites (++,*), on more northerly slopes (+, *), in shallower soils (*), and with increasing altitude (-,*). The relationships between clay, and aspect and altitude also have support from the soil analytical results from the Cedarberg transect. Of the 29 plots, only 5 had textures finer than loamy sand. Two of these were from the T.M. shaleband, whereas the other three were from low altitudes at the base of the southerly slopes. Bond (1981) also provides support for the occurrence of finer textures on south-facing slopes. He records loamy sands and sandy loams on the north aspects of the Outeniquas and sandy loams and sandy clay loams on the south aspects.

The above correlation analysis showing an east-west gradient in clay content comes from the estimations of clay content in each plot. These results are confirmed by the soil analyses, but the soil analyses also show that other fine-grained soil particles (silt and fine sand) increase towards the east (Table 7). Throughout the western zone, the T.M. quartzites mostly give rise to medium (and some coarse) sands and loamy sands (e.g. means of 5,1% clay, 5,2% silt and 30,5% fine sand; CE, n= 29). In the south east one still finds sands, but textures are mostly fine sandy loams and medium sandy loams (e.g. 9,0% clay, 13,1% silt, 47,8% fine sand; BA, WE & EL, n = 9). On the Witteberg quartzites a similar gradient is apparent. In the west (SW, GY), there are coarse-textured soils, mostly medium sands and medium loamy sands, whereas in the east (SU, GR) the textures are mostly fine sandy loams (e.g. 4,6% clay, 4,6% silt, 49,0% fine sand in the west, n = 4; and 11,1% clay, 15,2% silt, and 54,2% fine sand in the east, n = 8). In general, the Witteberg quartzites appear to be finer textured than the T.M. quartzites, at least from the Witteberg Mountains eastwards.

The soils recorded with the finest texture (sandy clay loams, clay loams, loams, silt loams; in 40 of the 507 plots) are mostly associated with two distinct environmental situations (χ^2 = 136, d.f. = 2, p <0, 001). Sandy clay loams and clay loams are usually found associated with the organic soils of the south-facing slopes of the coastal ranges. The upper shaleband of the T.M. Group usually has sandy clay loams but its texture is very dependant on the amount of quarzitic colluvium present. For example, in the Cedarberg, the two shaleband plots had soils with a higher clay and silt content than other plots on the transect but were nevertheless only medium sandy loams (as opposed to medium loamy sands on the quartzites). The Tchando Formation of the T.M. quartzites appears to sometimes give rise to soils with a texture finer than that of the soils derived from the other quartzitic formations. However, the χ^2 was not significant probably due to insufficient data (the Tchando formation was the recognized quartzite in 19 plots). Fine-textured soils (e.g. sandy clay loams) are also a feature of the Witteberg and T.M. quartzites of the south-east (e.g. BA, WE, GR transects).

Soil types

The only major published works on soil types in the mountains of the Fynbos Biome are those of Lambrechts (1979, and in Boucher, 1978) and

Kruger (1979a). In the account below, I discuss the distribution of types identified in the sample of 507 plots. The classification system used (MacVicar *et al.*, 1977) and the diagnostic features of the soil forms identified are shown in Fig. 6. Many plots would probably have been assigned to a rocky-land class by a pedologist, rather than to a soil type, but this does result in an information loss, for plants undoubtedly grow in rocky soils, and classifying soils as incipient Mispahs or Cartrefs does provide some information about different edaphic conditions. I have therefore been generous in assigning very rocky soils to soil types.

The most common forms present (Fig. 7) are Mispah, Glenrosa and Cartref (31%, 18% and 9% occurrence respectively). These three forms are all litholic in the study area, and make up the bulk of the shallower soils (<0, 4 m) that were recorded (Fig. 8). The Cartref form, represented by the series with low clay contents, is especially a feature of the coastal ranges, from the south west (HA, HE, HO) to the extreme east (EL) and is usually found at the higher altitudes. Associated with Cartref, either on the better drained steeper sites, or at lower altitudes on the north aspects, are soils of the Mispah and Glenrosa form. These latter forms are also the dominant forms on the interior ranges including those of Witteberg quartzite.

In the Glenrosa Form it is the coarse-textured series that are the rule in the West (e.g. Oribi Gsll), whereas in the east it is the more medium-textured series that are found (e.g. Kanonkop Gs13, Platt Gs14 and Trevanian Gs17). On the Witteberg quartzites of the south-east (SU and GR) the Mispah form is uncommon and better developed soils are found (e.g. Glenrosa, Oakleaf, Nomanci, the last being a typical mist belt and grassland soil). On three of the ranges comprised of Witteberg quartzite (GR, SU, WI) even the heavy-textured Swartland

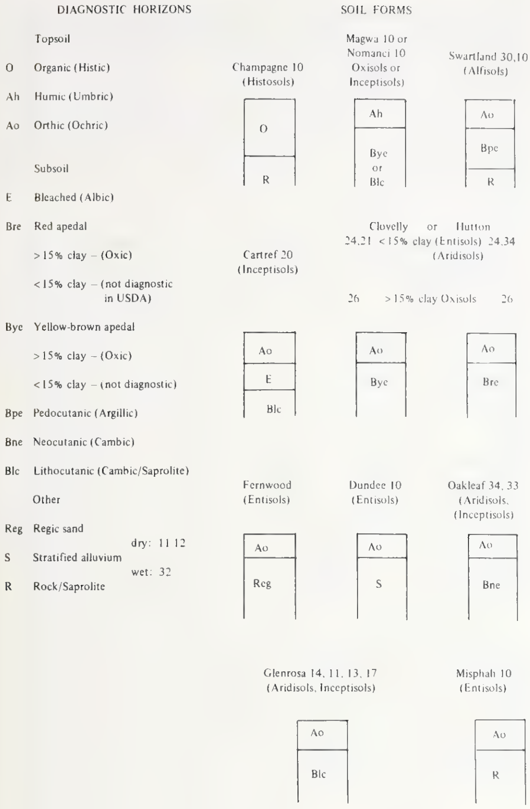

FIG. 6.—The principal soil forms recorded in the study, and their defining characteristics. The South African soil classification system subdivides soils into soil forms on the basis of defined diagnostic soil horizons. Each form is subdivided into series according to texture, base status etc. Approximate U.S. Dept. of Agriculture (1960) equivalents are given in brackets. Some of the major soil series recorded are indicated by their soil series numbers.

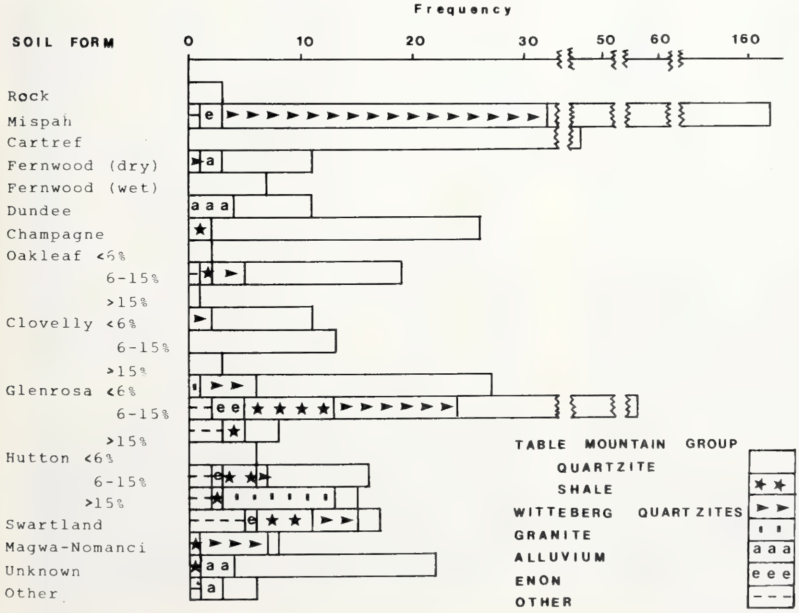

FIG. 7.—Frequency of soil forms and their relationship to geology. Percentages refer to percentage clay content and are the limits recognized in the soil classification system.

form was identified. Its occurrence is probably due to the presence of minor shalebands in the quartzites. Of the Mispah, Glenrosa and Cartref forms, it is only the Glenrosa which occurs to any degree on the non-quartzite geological formations in the study area.

After these three types, the next most common soil forms of the open slopes (TOP = 1) of the quartzites are the relatively deep Clovelly, Hutton and Oakleaf Forms (Figs 7 & 8). These forms are generally found on the lower slopes, on more southerly aspects and on gentler slopes. In the west they are more a feature of the interior ranges. If on north slopes, they are usually restricted to talus slopes, colluvial fans or pediments. The Clovelly Form with its yellow-brown apedal B horizon is more common in the north-west (e.g. Cedarberg), whereas the Hutton Form with its red apedal B horizon is more common in the south (e.g. the deep Hutton's on the south facing-slopes of the southern coastal mountains). However, the red apedal/yellow-brown apedal distinction is not easily correlated with distinct environmental situations (MacVicar *et al.*, 1977, discuss the supposed distinctions). The Hutton and Clovelly Forms are represented mostly by the coarse- and medium-textured mesotrophic series (e.g. Sonneblom Cv21, Springfield Cv24, Clansthal Hu24). The Oakleaf Form is apparently a feature of the south and south-east. However, it is a rather unsatisfactory form, at least as recognized by myself, for it includes very diverse soil profiles.

Of the major soil types mentioned so far those showing more advanced pedogenesis are associated with the more southerly aspects, the gentler slopes and the lower altitudes. As indicated earlier these situations are also the situations where deeper soils with less rock cover and perhaps higher clay contents occur. The catena that can be expected from situations where soils are least developed to where they are best developed is: [Mispah] [Glenrosa, Cartref] [Hutton, Clovelly, Oakleaf]. Of course, it is not the case that all the forms will be found on a single catena, e.g. the Cartref Form is more or less restricted to the coastal mountains.

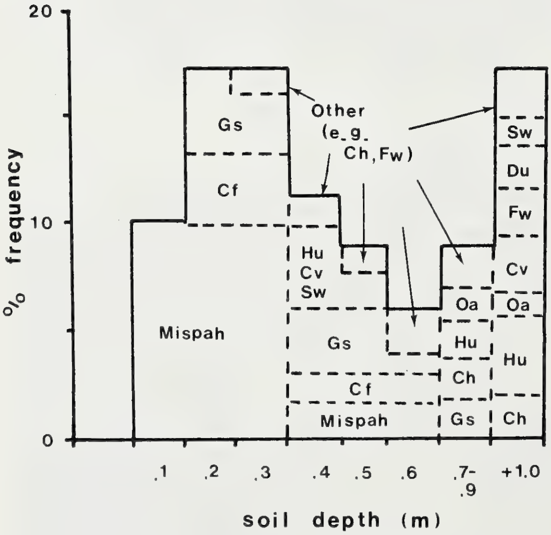

FIG. 8.—Frequency of soil depth and relationships between soil depth and soil form. The soil form distribution among soil depths has been determined for the following depth classes: 0,1–0,3 m, 0,4–0,6 m, 0,7–0,9 m and > 1,0 m. Soil forms abbreviated as follows: Cf., Cartref; Ch, Champagne; Cv, Clovelly; Du, Dundee; Fw, Fernwood; Gs, Glenrosa; Hu, Hutton; Oa, Oakleaf; Sw, Swartland.

The remaining soils that are common on the quartzites are generally not found on the open slopes (i.e. not TOP = 1). Especially common in the west are the deep (often > 1 m) coarse white sands of the dry plateaux. These belong to the Fernwood Form (Fernwood and Sandveld series—Fw11 & Fw12). In the north west where rainfall is lower and soils are richer in iron oxides (Lambrechts, 1979), the Fernwood Form is often replaced on the plateaux by deep, yellow sands of the Clovelly Form. Where the watertable is close to the surface on the plateaux, organic matter accumulates and the soils then belong mostly to the Trafalgar Series (Fw32) of the Fernwood Form. Under situations where profiles are perenially wet, peat-like horizons develop, giving rise to soils of the Champagne Form. These are mostly restricted to the wet south west if on plateaux, to riparian habitats of the coastal mountains, and to the south aspects of the coastal mountains. This last habitat becomes almost zonal, e.g. as on the south aspects of the high peaks of the south-west and as on the lower south slopes of the Tsitsikama Mountains. Associated with the Champagne Form on these south aspects, but also often found on the south aspects of the higher interior peaks, is a 'humic' Mispah. It is a very rocky soil, but it has a high oxidizable carbon content (*c.* 5%) Kruger (1974) and Bond (1981) also note its presence. A humic phace of a Cartref can also be recognized. Alluvial terraces throughout the study area, mostly derived from quartzite, give rise to the Dundee Form.

A different suite of soils, at least at the series level, is associated with the non-quartzitic rocks. On the upper Table Mountain shaleband a common form is Glenrosa represented by the more medium-textured series (e.g. Platt Gs14). On concave shaleband slopes and where the shaleband soils are not mixed with quartzitic colluvium, the Swartland Form is found (e.g. Rosehill Sw30). Other shaleband soil forms include medium-textured Hutton and Oakleaf members, and on the moister sites, Longlands, Estcourt and Magwa (cf. Boucher, 1978). On granites and shales, soils of the Hutton and Swartland forms are common. Most granite soils of the study area belong to the Hutton form (Msinga Series Hu26).

Soil chemistry

The soils of the T.M. quartzites are extremely acidic and have low exchangeable cations (S-value), low total nitrogen and low available phosphorus (Table 6). Oxidizable carbon ranges from less than 1% to over 13%, the high values being recorded in the peat-like Champagne form. These latter soils had the lowest recorded pH values (pH<3,4).

The PCA of soil textural and chemical variables summarizes the variation encountered (Fig. 9). The major gradient that is identified in Fig. 9 (by the first and second principal components) is associated with the west-east gradient (Table 7). In the west, one has course-textured soils with higher available phosphorus, whereas in the east one has finer textured soils (high proportions of clay, silt and fine sand) which have a higher pH and S-value. Nine of the samples from soils of the T.M. quartzites have S-values above 4 me/100 g soil and all of these are found in the eastern and southern Cape. The third principal component identifies the other major gradient in the soil variables. Carbon and nitrogen are strongly positively correlated (Fig. 9) and their variation is chiefly accounted for by altitude and rainfall with which they are positively correlated (Table 7). Carbon and nitrogen are also strongly associated with some variables of the first gradient. Both are positively correlated with S-value (r = 0,35 and r = 0,46 respectively), but carbon is strongly negatively correlated with pH (r= −0,40). Note, however, that S value is primarily associated with clay content (r = 0,66). A PCA using the Cedarberg data indicates independence of texture and soil chemistry (Fig. 10). These quartzitic soils have low clay and silt contents, and the variation in pH, nitrogen, phosphorus and S-value is related to organic content. pH is at the negative pole of the first component and the other variables are at the positive pole. This is mainly a result of a strong negative correlation between pH and carbon (r = −0, 58).

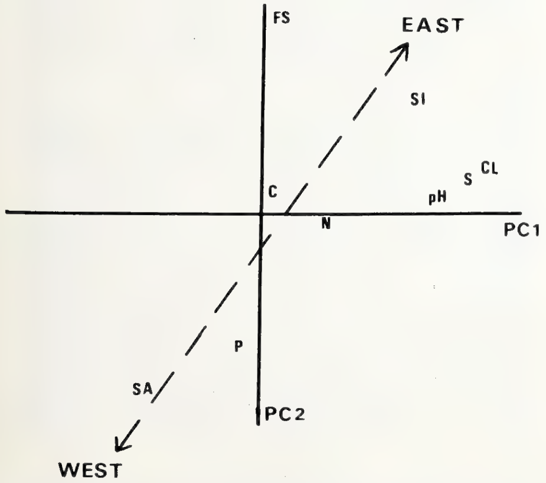

FIG. 9.—The first two principal components (PC) of soil variables. The west-east interpretation of these components is shown. The third component, not shown here, identifies N and C as covarying environmental variables and these are interpreted as being associated with the altitude — rainfall gradient. The analysis was done on the T.M. quartzitic soils (data as for Table 6, n = 51). Results from other subsets of the data from the T.M. quartzites showed almost identical results. The first 3 components account for 69% of the variance (37%, 18%, and 14% respectively). Abbreviations as in Table 2 (SA = MS + CS).

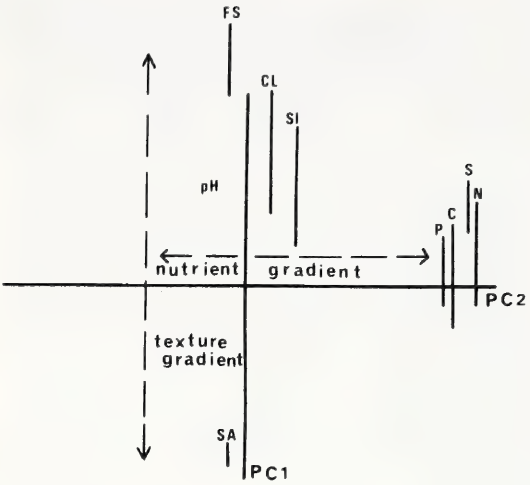

FIG. 10.—The first three principal components (PC) of the PCA of soil variables for the Cedarberg plots (n = 29). The third component is represented by the vertical bars. Results from other subsets of the data from the Cedarberg showed almost identical results. The first three components account for 75% of the variance (39%, 24% and 12% respectively). Abbreviations as in Table 2 (SA = MS + CS).

The results above refer to the soils of the T.M. quartzites. The data available (Table 6) are insufficient to provide stringent tests of differences between geological types as the sample sizes for the groups other than the T.M. quartzites are too small. However, F tests between types indicate that textural variables (especially clay and fine sand) are more important in differentiating between geological types than are chemical variables. For instance, clay content is the only variable that differs significantly between T.M. quartzites and non-quartzites (F = 22,9, df = 1 & 56, p<0,001). Variables that are nearly significant are S-value (p = 0,07), medium sand (p = 0,13), silt (p = 0,14) and pH (p = 0,16).

SYNTHESIS

To synthesize some of the foregoing, PCA was applied. In the PCA with all plots included, the first component represents the rockiness-soil depth gradient (Fig. 11). At the one extreme are the gentle slopes of the foot-hills, plateaux and valley floors with their deep, less rocky soils. At the other extreme are the steep slopes with their litholic soils. The second component represents the regional climatic gradients. It includes both the west-east gradient and the coast-interior gradient, and associated with it are altitude (highest in the interior) and clay (highest in the east). The third component represents a rainfall-rockiness gradient. Because percentage winter rainfall is associated with it, it is regional gradient rather than a gradient representing the altitude-rainfall gradient of individual transects. This PCA may be confounding regional gradients and local gradients and thus further interpretation is difficult.

In the principal components analyses of representative transects an altitude-rainfall gradient is always extracted. Apart from rainfall and altitude, few variables are consistently associated with this gradient. Clay contents are usually higher where

TABLE 6.—Mean values of various soil variables in the different geological types. The peat-like soils (mostly intrazonal, carbon >7,0%) and two outliers from the T. M. quartzites are excluded. The non-quartzitic group includes a range of different geological types: T. M. shaleband (n = 3), Enon conglomerate (n = 2); and two other shale types (n = 2). The samples from the Witteberg quartzite come mainly from the east (8 of 12)

	T. M. quartzites		Witteberg quartzites		Non-quartzites	
	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S. D.
S value (me/100g soil)	2,0	1,62	3,4	1,87	3,2	2,01
Total N (%)	0,07	0,038	0,08	0,049	0,09	0,043
Available P (ppm)	11,9	6,22	10,1	4,26	13,7	10,09
Oxidisable carbon (%)	3,2	1,69	3,5	2,09	3,3	1,81
pH	4,1	0,38	4,3	0,17	4,3	0,39
Coarse sand (%)	13		6		13	
Medium sand (%)	36		20		28	
Fine sand (%)	36		52		32	
Silt (%)	8		12		12	
Clay (%)	7		10		15	
n	**51**		**12**		**7**	

TABLE 7.—Correlation coefficients between soil variables and altitude, annual rainfall, percentage winter rainfall and transect number for the plots of the T. M. quartzites (n = 51, data as for Table 6). The bracketed results are from the Cedarberg (n = 26). The symbols indicate strength of positive and negative correlations. There was insufficient data to do correlations with variables such as aspect

	Annual rainfall	Altitude	% winter rainfall	Transect number
Total nitrogen	+++ (+++)	(+++)		
Oxidisable carbon	+++ (+++)	(+++)		
S Value	-		---	+++
pH	--- (--)	- (-)	--	++
Clay	(+)	-	--	++
Silt			---	+++
Fine Sand		---	---	+++
Medium sand		+++ (+)	+++	---
Course sand		+	++	--
Available phosphorus		+++	---	

+ or - $p<0,05$; $r>0,27$ (0,38)
++ or -- $p<0,01$; $r>0,35$ (0,49)
+++ or --- $p<0,001$; $r>0,44$ (0,60)

altitudes and rainfall are lower. The other components represent different aspects of the rockiness-soil depth gradient.

PCA is supposedly a useful tool for summarizing variation of environmental data, for environmental variables are usually linearly related (e.g. Bouxin, 1976; Green, 1979; Orloci, 1975). However, because PCA attempts to summarize variation in as few dimensions as possible, some distortion must occur. This is one reason why I have found that a full understanding of the interrelationships between variables requires the direct examination of correlation matrices, rather than the examination of the principal component summary of the matrix. Another reason why I found PCA unsatisfactory was the absence of a technique to combine PCA's from individual transects into a single statement of the trend within transects. Fisher's (1970) technique for combining correlation matrices was extremely useful for providing this single statement but unlike PCA, it requires direct examination of relationships between variables, In the summary below, I have relied more on the results of the previous sections than on the PCA's reported above.

The variation of environmental variables in the study area can be summarized as follows. One set of gradients in the study area are the regional gradients — the west-east gradient and coast-interior gradient. They are correlated with each other, and although chiefly climatic, also consist of a number of topographic and soil variables (Fig. 12a). The other set of gradients are those within a single transect. The rockiness-soil depth gradient with its often associated variables (rock cover, soil depth, clay

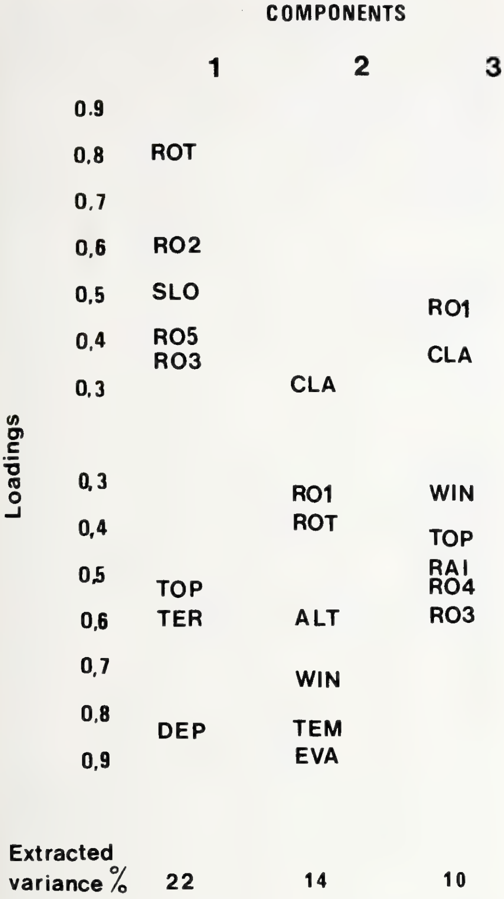

FIG. 11.—Principal components analysis of all plots. Abbreviations as in Table 1. Variables not strongly correlated with a particular component are not shown (– 0,3 < loading < 0,3).

content and slope), is found in three situations, Firstly, it is associated with the altitude-rainfall gradient; secondly, it is associated with the gradient from southerly to northerly aspects and finally, it is associated with local topographic variation (e.g. at any altitude on any aspect it can be found on the gradient from slope to plateau). Fig. 12b summarizes the gradients on a generalized mountain transect. Apart from these gradients there are also the distinctions between geological types. In the quartzitic soils, at least those of the T.M. group, soil depths tend to be shallower than in the non-quartzites, and textures are coarser.

DISCUSSION

Weathering, denudation and pedogenesis

Most of the gradients identified include both climatic and edaphic variables and in most cases the covarying variables are causally related. Perhaps one major exception is the relationship between percentage winter rainfall and soil texture. The texture gradient from west to east is probably a consequence of the manner in which the sediments comprising the quartzites were laid-down (Rust, 1967) and may have little to do with climatic control of pedogenesis, even though one would expect more intense weathering in the summer rainfall regions of the east. The percentage winter rainfall-texture correlation has important implications for vegetation-environment studies: how does one separate the climatic and edaphic effects? Both nutrient conditions (probably related to clay content) and percentage winter rainfall have been implicated as major controlling factors in fynbos structure (Kruger, 1979a). That the soils of the Witteberg quartzites are on average finer textured than those of the T.M. quartzites could also be explained by the manner in which the sediments were laid-down. However, the presence of numerous minor shale-bands in the Witteberg quartzites and the mixing of shale-derived and quartzites-derived material in the soil profile has undoubtedly also resulted in a number of soils of finer textures.

Holland & Steyn (1975) draw attention to the marked vegetation differences on north and south aspects in the Biome and interpret them in terms of differences in soil moisture and ambient temperature and ultimately in terms or radiation loads. Any explanation of the vegetation differences must surely also include the differences in soil development. Because of lower plant cover (Bond, 1981; Campbell, in press b) and lower soil moisture contents on the north aspects one can expect, on the north aspects, lower rates of chemical weathering, a higher degree of sheet erosion and minimal soil development (Bond, 1981; Garland, 1979). These processes probably explain the aspect gradient recorded in this study (Fig 12b). Garland (1979) suggests that a similar scenario has led to the geomorphological asymmetry observed in Drakensberg valleys, where north aspects are less steep than south aspects. As stated earlier there is a slight indication of asymmetry in the present study. However, slope inclination in the present study area is probably more a function of the orogenic processes that have occurred and the extreme resistance of the quartzites to weathering.

Climatic control of the denudation process is indicated by some of the differences between the dry hot interior (e.g. the north-west) and the humid cool coastal mountains (e.g. the south). In the south, especially the south aspects, the slopes are well vegetated and the debris mantle appears to be stable. In the north-west plant cover is low (Campbell, in press b), and there is much evidence of mass wastage, including rock and debris falls, and talus and soil creep. The rocky landscapes of the north west consist of precipitous cliffs and extensive colluvial fans. Prominent cliffs are not a feature of the south.

The importance of summer mists for fynbos has long been recognized (references in Kruger, 1979a). Mists are also important in soil development as is indicated by the location of soils of the Champagne Form on the south aspects of the high peaks of the coast. These slopes are permanently saturated by the winter rains and summer mists thus following an organic horizon to develop.

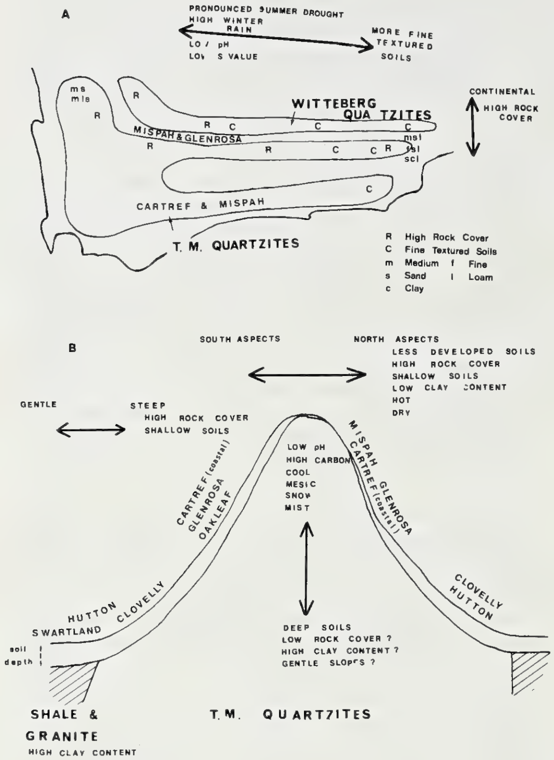

FIG. 12.—Summary of the gradients recognized. A, regional gradients; B, gradients on an idealized mountain. Questionable relationships are indicated.

Nutrient-poor soils

The quartzite/non-quartzite distinction occurring in the Fynbos Biome is often seen as corresponding to a nutrient-poor/nutrient-rich distinction (e.g. Kruger, 1979a; Boucher & Moll 1981; contributions in Day, 1982). The results presented here suggest it is mostly soil textural variables and not chemical variables which distinguish the quartzite-derived soils from the non-quartzitic soils. However, my sample of non-quartzitic soils is small and does include Enon conglomerates which Cowling (1983) records as being of a similar fertility to T.M. quartzites. Low (pers, comm.) and Cowling (1983) have demonstrated very different fertility levels between soils from T.M. quartzites and soils from Malmesbury or Bokkeveld shales. Nevertheless caution should be exercised when substituting the nutrient-poor/nutrient-rich distinction for the quartzite/non-quartzite distinction, at least in the mountains.

The working definition of a nutrient-poor soil at a recent symposium (Day, 1982) included the following: pH less than 6,0; total nitrogen less than 0,12%; and sum of exchangeable cations (S-value) less than 7me/100 g soil. Almost all the soils of the present study (e.g. Table 6) would be classified as nutrient-poor including those of the non-quartzites (a number do not qualify on the total N requirements, but some of these are peat-like soils and would not be regarded as nutrient-rich). Even though the soils would be classified as nutrient-poor, they often support non-fynbos vegetation, a situation which contradicts Specht & Moll's (1982) conception of the contrasting plant communities that are associated with nutrient-poor and nutrient-rich soils. Either the definition of nutrient-poor is at fault or Specht & Moll's (1982) conception is inadequate.

Kruger's (1974) data from a south-west catchment indicate that cation exchange capacity and S-value are strongly correlated with oxidisable carbon and Kruger therefore suggests that fertility in the quartzites depends largely on plant remains in the soil. The result's from the Cedarberg support this finding. However, in the sample as a whole (T.M. quartzites) texture is more important in determining S-value. It is the soils of the east that have the higher clay contents, higher S-value and higher pH values. Therefore, within a transect, soil fertility may be closely tied to plant remains (with organic matter generally higher at higher elevations — this study; Bond 1981; Kruger, 1974), whereas in the Biome as a whole, texture is important in determining fertility, or at least, in determining S-value and pH. pH is consistantly negatively correlated with carbon (this study; Bond, 1981). This is perhaps related to the release of organic acids from organic matter and would definitely be the case in the organic soils. However, carbon does not explain most of the variation of pH in the quartzitic-derived soils; much of the variation, at least at the regional level, is related to soil texture, and ultimately to leaching. Even the carbon-pH correlation may not be casual. Carbon is high and pH is low at high altitudes; the low pH perhaps being determined by higher leaching at high altitudes, and the high carbon probably being determined by lower decomposition rates (Bond, 1981). Available phosphorus as measured by Bray No. 2 is higher in the west and is positively correlated with coarse and medium sand. This pattern has no clear explanation.

Considering the importance placed on nutrients in determining fynbos structure (e.g. Specht & Moll, 1982) it is critical that more work in this direction be undertaken. The present study lacks details with regards to nutrient conditions – too few samples, only one sample per profile and no bulk densities. Bulk densities are especially lacking considering the high degree of rockiness in soil profiles.

Methodology and mythology

A quantitive approach to fynbos environments has been taken by few researchers. Kruger (1974) provides a topographic analysis and some correlations between soil chemical variables and topographic variables for a catchment in the south-west. Bond (1981) in a parallel study to my study, has done a detailed environmental analysis of two of the transect sites that I have studied (OU and GS). Apart from the above the only published account of soils of a specific mountain area is that in Boucher (1978), and that includes no analytical results. The lack of data on Fynbos environments has ensured the development of a number of myths, some of which are discussed below.

Soil depths are usually considered to be extremely shallow (e.g. less than 30 cm — Boucher & Moll, 1981). Average soil depth recorded in this study was 0,5 m. If the soils from non-quartzitic geological types are excluded from the sample then the average depth is still greater than 0,4 m. And even this is an underestimation because of the difficulty of excavating rocky profiles (Bond, 1981). Of the 17 profiles described by Bond (1981), only 40% are less than or equal to 0,5 m in depth.

Kruger (1979b) states that the fynbos soils are mostly lithosols, podzolica and podzols. Lithosols are indeed the case, for as recognized here most of the Cartref, Glenrosa and Mispah Form are litholic. A pedologist would probably map much of the study area as 'Rock/Mispah' complexes (Bond, pers. comm.). The importance of podzolization is apparently overstated. The only dominant soil form which approaches a podzol is the Cartref. It has a bleached E horizon, and it would sometimes be regarded as a true podzol as is evidence by an incipient ferrihumic B horizon (Houwhoek Form). But the Cartref is only a dominant soil form in the coastal mountains. The interior mountains show podzolization very rarely. In the southern Cape, Bond & D. Grey (pers. comm.) almost only find podzolic features on the south aspects of the coastal mountains (e.g. weak accumulation of ferrihumic material even in the deep Hutton soils).

Soil colour is usually considered to be greyish (grey, dark grey, grey brown etc. – e.g. Kruger 1979a, 1979b, Boucher & Moll 1981). 67% of the Cedarberg plots have soils other than greyish (e.g. yellow-brown, brown). The only area where greyish soils predominate are in the coastal mountains especially in the south-west. Even the coastal mountains of the south had a high proportion of non-greyish soils (e.g. many browns, reds and yellows). I would estimate that greyish soils comprise less than 50% of the present sample.

Most of the generalizations about fynbos have been derived from research undertaken in the south-western area and, as shown here, many of the generalizations about soils do not hold in other areas of the biome. The generalizations about soils tend to understate the complexity that occurs within the Biome and may result in the tendency to disregard soils in phytosociological studies of fynbos. Most plant community studies in the Biome have stressed phytosociological relationships to the near exclusion of community-environment relationships. For instance, there are almost no quantitative statements about rock cover. Most studies only include information on altitude, aspect and slope. Bond (1981) and Campbell (in press a) present hypotheses about fynbos vegetation structure which stress the importance of soils.

Bond's (1981) account of environmental gradients provides support for most of my generalizations about trends within transects (as summarized in Fig. 12b). Perhaps the major difference is Bond's stress on the aspect gradient. In his PCA's the aspect gradient is always extracted as the first principal component, i.e. it accounts for most of the variance in the measured variables. My PCA's of individual transects, and all plots, do not usually extract the aspect gradient as the first principal component. This means no more than that Bond's selection of variables for the analyses differed from mine. The importance of the gradients to the plants can only be measured by using biological data; as Mason & Langenheim (1957) state, an environment is only an environment because it is organism-directed.

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UITTREKSEL

Omgewingsdata versamel op 507 persele op 11 dwars deursnitte, en grond-analise van 81 van hierdie persele is gebruik om die plantomgewings van die berge in die Fynbos-Bioom te beskryf.

Twee hoof- streek gradiënte word herken: 'n wes-oos gradiënt en 'n kus-binnelandse gradiënt. Van besondere belang vir fynbosomgewingstudies is die toename in die verhouding van fyn gronddeeltjies van wes na oos. Minstens sommige aspekte van grondvrugbaarheid vermeerder ook na die ooste toe. Die edafiese veranderinge is parallel aan klimaatsveranderinge: hoofsaaklik 'n afname in die felheid van somerdroogte in 'n oostelike rigting. Op die kus-binnelandse gradiënt is die rotsbedekking 'n belangrike nie-klimatiese veranderlike. Hoë rotsbedekking is 'n kenmerk van die binnelandse reekse. Grond met organiese horisonne of met E-horisonne is 'n kenmerk van die berge van die kus, maar ontbreek dikwels op die binnelandse berge.

Die ander omgewingsgradiënte wat herken is, kom voor op individuele dwars deursnitte en almal sluit edafiese veranderlikes in. Die rotsagtigheid-gronddiepte-gradiënt, waar 'n toename in rotsagtigheid geassosieer word met 'n afname in gronddiepte en gewoonlik 'n afname in klei-inhoud, neig om in drie situasies voor te kom. Eerstens, word dit geassosieer met lokale topografiese variasie; die vlak, rotsagtige grond is 'n kenmerk van die steiler hellings. Tweedens, word dit geassosieer met die hellinggradiënt; die warm, droë noordelike hellings het vlakker, rotsagtige en minder ontwikkelde gronde. Derdens, neig dit om geassosieer te wees met die hoogte-reënvalgradiënt; vlakker gronde word op hoër hoogtes gevind. Dit is ook op hoër hoogtes waar hoër reënval gevind word. Variasies in oksideerbare koolstof word hoofsaaklik toegeskryf aan die hoogte-reënvalgradiënt. Terwyl aspekte van grondvrugbaarheid op 'n bioomwye vlak verband hou met grondtekstuur, blyk dit op individuele dwars deursnitte dat vrugbaarheid verband hou met hoeveelhede plantoorblyfsels teenwoordig in die grond, en met reënval.

Afgesien van hierdie gradiënte, wat op die Tafelberg-kwartsiete gevind is, is ander bronne van omgewingsvariasie die gevolg van verskille tussen geologiese tipes. Die nie-kwartsietiese gronde is oor die algemeen dieper en van fyner tekstuur. Dit word voorgestel dat die voedingstofryke en voedingstofarme onderskeiding met groot omsigtigheid toegepas moet word: die onderskeiding behoort, minstens in die berge, nie outomaties vervang te word deur die kwartsietiese/nie-kwartsietiese onderskeiding nie.

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A homogeneity index based on species diversity in Sour Bushveld

R.H. WESTFALL*, N. VAN ROOYEN** and G.K. THERON**

ABSTRACT

The co-efficient of variation (CV) for the linear regressions of species-area curves, on a linear species number/log area scale, for the samples in a community, appears to indicate the homogeneity of the community. A CV of less than 15% appears to indicate homogeneous vegetation while a CV greater than 15% seems to be indicative of vegetation heterogeneity, as correlated with extremes in recorded environmental factors in Sour Bushveld.

INTRODUCTION

The plant ecology of the farm Groothoek, Thabazimbi District, was studied in order to supply data on the Sour Bushveld (Acocks, 1975) on natural resource inventory for the Department of Agriculture's Natural Resources Classification. The study included classification of the vegetation according to the Zürich-Montpellier approach (Werger, 1974) as well as alpha and beta diversities according to Whittaker *et al.* (1979). Alpha diversity refers to the number of species in a community (Whittaker, 1972), whereas the rate of increase in species number with increasing area is also characteristic of a community and is indicative of dispersion (Whittaker *et al.*, 1979).

Both species number and rate of increase can be illustrated by means of a linear regression of the species-area curve on a linear species-number/log area scale (Whittaker *et al.*, 1979).

Many attempts have been made to quantify vegetation homogeneity (Raabe, 1952; Curtis, 1959; Dahl, 1960 and Moravec, 1971), however, there has been no satisfactory objective method (Mueller-Dombois & Ellenberg, 1974). In this study, the relative homogeneity of the plant communities is assessed after the classification of the vegetation.

STUDY AREA

The study area is the farm Groothoek 278KQ situated in the south-western Waterberg area of the Transvaal between southern latitudes 24° 28' and 24° 31' and eastern longitudes 27° 32' and 27° 39'. The original farm Groothoek, which has subsequently been subdivided into a number of small farms covers approximately 4 000 ha.

The study area varies in altitude from 1 050 to 2 080 m. The soils are mainly of the Mispah Form, Mispah Series. Also locally present are: Shortlands Form, Bokuil Series; Hutton Form, Middelburg Series; Westleigh Form, Sibasa Series and Kroonstad Form, Slangkop Series. The soils are derived from sandstone conglomerate and shale of the Waterberg Group as well as post-Waterberg diabase. The vegetation is described by Acocks (1975) as Sour Bushveld, with an outlier of North-Eastern Mountain Sourveld above 1 600 m altitude.

METHODS

Analysis

A total of 170 quadrats, each measuring 10 m × 20 m, was distributed on a stratified random sampling basis throughout the study area for classifying the vegetation. Species diversity data (Whittaker *et al.*, 1979) were obtained by recording species presence in nested quadrats within each 10 m × 20 m quadrat. Five 1 m × 1 m, one 2 m × 5 m and one 10 m × 10 m subsamples within each 10 m × 20 m quadrat were used. All permanently recognizable species were recorded in each quadrat.

Habitat data recorded at each sample site included altitude, geological formation, aspect, slope, soil depth, soil form and series, geomorphology, vegetation structure and estimated percentage surface rock cover. Soil samples were collected for later chemical analysis.

Synthesis

The vegetation was classified into communities and sub-communities with the aid of the PHYTOTAB program (Westfall *et al.*, 1982) and the condition of the vegetation with respect to grazing was assessed (Westfall *et al.*, 1983). The species diversity for each quadrat was determined by the linear regression of the species area curve, on a linear species-number/log area scale. Species number is plotted on the ordinate with the log of the area, in square metres, on the abscissa. The log area scale, therefore, reads: 0 (1 m^2); 1 (10 m^2); 2 (100 m^2) and 2,3 (200 m^2). The species number for 1 m^2 was taken as the average of the five 1 m^2 subsamples for each quadrat.

The species number was extrapolated to log 3 (1 000 m^2), because this range can be extrapolated to allow standard comparisons (Whittaker *et al.*, 1979). The co-efficient of variation (CV) was calculated for the variation in species number at log 3 of the quadrats in each community. The communities were then listed according to their CV and comparisons were made with recorded environmental factors.

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RESULTS

The listing of communities according to their quadrat CV is given in Table 1 together with the environmental factors which have a sufficiently wide variation within a community to possibly account for the high CV. The following factors appear to be significant (Table 1):

(i) Veld condition assessment, composition score, which is the lowest for communities 4 and 7. The composition score is derived from a benchmark within the community and the sample quadrats (Westfall *et al.*, 1983), the low score indicating a large floristic difference between benchmark and sample quadrats, because of different levels of overgrazing.

(ii) The sum of the standard deviations for the veld condition classes of the quadrats in each community is indicative of the uniform utilization of a community. Where the sum of the standard deviations is large, as in communities 7 and 16, overgrazing in parts of the communities can be expected. Waterlogging in parts of Community 16 during the rainy period as well as the camp system employed could account for the differential use, and overgrazing in Community 7 takes place in the vicinity of a kraal.

(iii) The slope ranges from 0° to 38° in Community 17b, which is the widest range in the study area. Drainage lines and interfluves on the upper slope of the mountain on which this community occurs, account for this range in slope.

(iv) The aspect of Community 18, being on the summit of a mountain, has the greatest variation in the study area.

(v) Variations in soil depth where the minimum recorded depth is greater than 69 mm or where the difference in soil-depth range is less than approximately 180 mm do not appear to influence vegetation homogeneity. Communities 9.2, 11.1 and 9.1 have shallow soils in parts and maximum recorded depths of 230 to 250 mm, which could influence vegetation homogeneity.

(vi) Surface rock cover has the greatest variation in Community 9.2 varying from 5–80%.

(vii) Soil electrical resistance has the greatest range in communities 17b, 11.1, 8.2 and 17a. These communities have moderate to steep slopes where nutrients could be leached from the upper areas and accumulate in the lower areas, accounting for the range in soil electrical resistance.

Community 8.1 does not have a single recorded habitat factor which could account for the high CV. However, a combination of habitat factors or possibly a single factor, not recorded, could be responsible. Community 2 is situated on the escarpment in the west of the study area. Although regarded as kloof forest the landform is heterogeneous with cattle able to graze in places. The heterogeneity of the landform, although difficult to quantify as extreme, could account for the high CV in Community 2.

TABLE 1. – Homogeneity of the plant communities on the farm Groothoek, Thabazimbi District, according to the CV for quadrat diversity (extrapolated to 1 000 m^2), and correlated with extremes in recorded environmental conditions

Community number	Homogeneity index expressed as CV (%)		Veld condition assessment, composition score (%) Grassland	Woodland sparse	Woodland open	Woodland closed	Kloof forest	$\Sigma\ \sigma$ for veld condition classes	Difference in slope range (°)	Aspect range (°)	Soil * depth range (mm)	Difference in surface rock cover range (%)	Difference in soil electrical resistance range (ohms)
14	4,46				34								
5	9,66					21							
10	9,76				42						40–80		
12	10,62				42								
11.2	10,98				36								
1	12,70	Homogeneous					31						
6	13,77					26							
15	14,46				36								
13	14,69				45								
3	14,74						27						
4	15,65					**14**							
9.2	16,06					30					**50–230**	75	
17b	16,09			45					**38**				**3 900**
11.1	16,29								Less than 29		**40–230**		**4 600**
8.1	17,00				41			Less than 63		Less than 181		Less than 56	Less than 2 900
8.2	17,22	Heterogeneous			26						Minimum greater than 69		**3 200**
18	17,60		67							**270**	40–100		
7	18,87					**13**		72					
9.1	18,98					30					**40–250**		
17a	20,32			22									**3 700**
16	27,90		31					**70**					
2	29,71						19						
						Over-grazing		Unequal grazing	Exteme habitat conditions recorded in communities				

* The minimum soil depth recorded is 40 mm. A range greater than 179 mm from the minimum depth appears to influence homogeneity, therefore the range of 40–80 mm does not appear to be significant.

It appears, therefore, that a CV of 15% is an acceptable boundary between heterogeneous and homogeneous vegetation in Sour Bushveld, because no environmental heterogeneity (extremes in environmental factors) could be detected for the communities with a CV of less than 15%. The CV gradient represented in Table 1 is difficult to corroborate with the recorded environmental factors, but personal observation confirms the order of the communities regarding homogeneity.

DISCUSSION

The variations in species number (diversity) and the rate of increase in species with increasing area (dispersion) provide a simple method of determining homogeneity in a floristically defined community. The rate of increase in species with increasing area partly determines the species number at log 3 so that both parameters, diversity and dispersion, are taken into account.

In the study area the main environmental factors influencing vegetation homogeneity are grazing, slope, aspect, soil depth, surface rock cover and soil electrical resistance as an expression of soluble salts. Notably lacking in influence is soil form, where three communities in the homogeneous range have two different soil forms each. Communities 5 and 4 are structurally and floristically similar, the difference being that Community 4 is diagnosed by mainly weedy species. This is confirmed by the lower composition score and higher CV for Community 4. The difference is attributed to overgrazing in Community 4.

The homogeneity index, as expressed by the CV for the communities, is of particular importance when interpreting the composition scores. For example, Community 18 has a high composition score, but is relatively heterogeneous. Grazing management should, therefore, take the heterogeneity of the vegetation into account. The open woodlands have markedly higher composition scores and are generally less heterogeneous than the closed woodlands. This could be significant in timeous control of woody encroachment. Community 8.2, for example, although predominantly open, is closed in places.

The homogeneity index can also indicate sampling adequacy. In the floristic classification, Community 17a is represented by two quadrats only and is considered a variation of Community 17b. Community 16 is represented by 12 quadrats of which three are heavily infested with *Stoebe vulgaris*. The potential vegetation is grassland without *S. vulgaris,* however, and the high CV indicates the infestation. Community 2 is represented by eight quadrats. This community could consist of several communities, because of the topographic range, if studied in greater detail than in the present study. It is noteworthy that sampling adequacy in this study is suspect with a CV of greater than 20%. The remaining communities are considered to be adequately sampled.

CONCLUSIONS

The homogeneity index based on species diversity appears to be a simple, yet sensitive method for quantifying homogeneity in floristically defined communities, in Sour Bushveld. The homogeneity index can be of value in assessing veld condition and determining sampling adequacy. Further data will, however, have to be analysed to determine the adequacy of the suggested 15% criterion between homogeneous and heterogeneous vegetation in vegetation other than Sour Bushveld.

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UITTREKSEL

Die koëffisiënt van variasie (KV) van die liniêre regressies van spesies-area-kromme, volgens 'n liniêre spesies getal/log area skaal vir monsters binne 'n plant-gemeenskap blyk om die homogeniteit van die gemeenskap aan te dui. 'n KV van minder as 15% blyk om homogene plantegroei aan te dui terwyl 'n KV van hoër as 15% blyk om heterogene plantegroei aan te dui. Die KV-waardes van die gemeenskappe is met die uiterstes in aangetekende omgewingsfaktore vir elke gemeenskap gekorreleer.

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OBITUARY

JAN ERENS (1911–1982)

Born in Groningen, Holland, on 5 August 1911, Jan Erens came to South Africa with his family in July 1914, and shortly afterwards his father, who was a trained horticulturalist, acquired a property along the northern foothills of the Magaliesberg between Pretoria and Brits. Growing up in a country environment where he was used to hard work, Jan developed a deep love of the land and nature, and at the age of 15 he left school to help with his father's cut-flower and fruit-growing business. After a further period of training in a commercial nursery, he joined the Pretoria Parks Department on 6 February 1930 and was soon put in charge of the Department's nursery in the Fountains Valley.

On 1 July 1935 he was appointed to the then Division of Plant Industry under Dr I. B. Pole Evans and was responsible for the garden around the Division's headquarters at 590 Vermeulen Street, Pretoria. Here his interest in indigenous plants was stimulated by contact with Dr E. P. Phillips, Dr R. A. Dyer and Dr Inez Verdoorn. It was a period when the public were becoming increasingly conscious of the rich South African flora and Jan showed that he was quick and eager to absorb knowledge in this new field. At that time the Department of Agriculture's horticultural section was also part of the Division of Plant Industry, so he had the opportunity of gaining first-hand information on fruit and flower growing from leading authorities such as H. B. Terry, Dr Vincent Reynecke and Dr C. J. Strydom, which stood him in good stead in later years.

In 1937 and 1938 Dr Pole Evans undertook two major expeditions: in 1937 to Ngamiland and in 1938 (the year before his retirement) through east tropical Africa to Kenya and Uganda, reaching as far north as Lake Rudolph on the border of Ethiopia. On both expeditions he took C. J. J. van Rensburg to gather living material of promising grazing grasses and Jan Erens to make a general herbarium collection and to collect plants and seeds for garden purposes.

These expeditions resulted in the addition of about 2 000 herbarium specimens and over 500 collections for the garden. Many of the latter flowered in subsequent years and were figured in *Flowering plants of South Africa* from 1940 onwards. Of the 40 plates in Volume 20 (1940), 12 were from the East African expedition, and it was probably this influx of material from the north that prompted the change in the title of the journal to *Flowering plants of Africa* from Volume 25 (1945). A number of the plants were described as new, including two which commemorated the collectors: *Aloe pole-evansii* Christian and *A. erensii* Christian.

The great variety of indigenous plants being introduced into cultivation, often with widely different requirements, called for much experimentation and improvisation. It was the sort of challenge which Jan Erens (Fig. 1) enjoyed, and the large measure of success which he achieved is a reflection of his ability and dedication.

FIG. 1.—Jan Erens.

After a somewhat dormant period during the war years, botanical activity revived when Dr R. A. Dyer was appointed, in 1944, as Chief of what was then the Division of Botany and Plant Pathology, the old Division of Plant Industry having broken up into several constituent divisions on Pole Evans's retirement. The need for a botanic garden worthy of the Division had long been felt and, with the active support of Prof. Davel, Dean of the Agricultural Faculty of Pretoria University, a portion of the University Farm about 50 ha in extent was allocated for this purpose towards the end of 1945.

The initial laying out and development of the new garden were tackled with Jan Erens's usual enthusiasm and in 1947 he made the first plantings, which included the row of camelthorn trees between the present main building and the nursery, as well as the fine group of Acacias where the workshop is now situated. These stand as a monument to him which will last many years.

At the end of September 1949 he was appointed to the horticultural section of the Public Works Department, where he saw better opportunities for advancement. Starting as Head Gardener at the Union Buildings garden, he was soon placed in charge of the Pretoria region and, on 1 October 1967, he succeeded Mr Norman Mann as Control Superintendent, responsible for government gardens throughout South Africa. Through his personal example and leadership he did much to enhance the prestige of this section. In 1969 he represented his Department at the International Horticultural Congress held in Switzerland. He also acted in an advisory capacity to the Voortrekker Monument

Committee and to the South African War Graves Commission.

He was a foundation member of the Institute of Parks Administration and was President during the meeting of the Institute in Pretoria in 1971. As a committee member for twelve years and as a member of the Technical Training Subcommittee, he played an active part in furthering the Institute's objectives and, in particular, in improving the conditions of the learner horticulturalists.

In 1942 Dr Dyer persuaded him to become Honorary Secretary of the Pretoria Horticultural Society 'as a temporary measure,' a task which he undertook with distinction for the next 25 years, ending as President of the Society from 1967 to 1977. During this period he was the mainspring of the Society, tireless when it came to organizing their shows, and contributing regular articles to the Society's magazine which reflected his wide experience and extensive knowledge of horticulture. In these activities he was greatly helped by his wife Iris, who, in the early 1950's, was one of the pioneers in what was then a new trend in flower arranging. Together they wrote a book entitled 'Flowers for the Home and Garden' in which many of her artistic floral compositions are illustrated.

At the end of September 1974 he took his pension from the Public Works Department and rejoined the staff of the Botanical Research Institute, where he was helpful in many ways, but mainly in the nursery, propagating material for mass displays in the garden. He regularly supplied ornamental plants and flowers for the main building and one of his last contributions was the provision of pot-plants and flowers for the AETFAT meeting in the CSIR Conference Centre in January 1982. He died suddenly in the nursery on 5 February 1982 during a particularly trying spell of summer weather.

Throughout my long association with him as a colleague and fellow committee member, I have found him to be a staunch and generous friend who was prepared to work himself to a standstill in a good cause. He was sincere, upright and unselfish to a degree, often at the cost of personal sacrifice, but could not tolerate injustices, especially to those less privileged than himself. He will be remembered for his boundless energy and enthusiasm, his ready smile and his willingness to lend a helping hand wherever he could.

L. E. CODD

REVIEW OF THE WORK OF THE BOTANICAL RESEARCH INSTITUTE, 1981/1982

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INTRODUCTION

The highlight of the year undoubtedly was the AETFAT Congress held in January 1982. (Fig. 1) This meeting was financed by the Department of Agriculture and Fisheries and organized jointly by the Botanical Research Institute and the South African Association of Botanists with the assistance of the CSIR Symposium Secretariat.

The impact of the influx of eighty overseas botanists including some of the foremost authorities in the botanical field was considerable and will make itself felt for many years to come. The congress was a great social success and gained many friends for South Africa as a result of the exceptional hospitality shown to visitors and the greater insight they gained in the South African situation. More important, however, is the awareness of the progress made with botanical research in South Africa which has been gained by overseas botanists and the increased stature which the country thus stands to achieve.

The opportunity offered by the presence of a number of the world's most outstanding taxonomists was utilized by organizing a workshop on one of the most pressing botanical needs, namely the completion of the Flora of Southern Africa. The meeting resulted in an excellent document which dealt with the problem in a penetrating manner and makes practical recommendations to rectify the situation.

It is most gratifying that scientific productivity in the form of publications remains high. Ninety-two papers were, for instance, published by the staff of the Botanical Research Institute chiefly in Bothalia, the general house journal of this Institute. The quality of some of the publications was excellent and there seems to be a noticeable improvement in the papers as a result of the standard insisted on.

An event of particular significance was the creation of additional posts for the Ecology Section of the Botanical Research Institute. This should allow the botanical aspects of natural resource surveys to be placed on a sound footing once the posts have been adequately filled.

Two interesting and valuable works appeared during the year under review. The first is the long awaited 'Botanical Exploration of Southern Africa' by Mary Gunn and L.E.W. Codd. This book is the culmination of lifelong research on botanical collectors of Southern Africa by the first author, most ably amplified and written up by the second author. It will remain a standard work on the subject for many years to come.

The second work is the first part of the volume on mosses in the Flora of Southern Africa series. This amply illustrated work is a landmark study of Southern African mosses and the artist as well as the author R.E. Magill are to be congratulated.

The herbarium information data bank PRÉCIS II is operational, and useful results are beginning to appear. Refinement of the data is still needed.

Except for the vacant new ecology posts, botanical professional posts are all filled. Even so, the needs for botanical work are increasing and expansion will be urgently needed as soon as the economic situation improves.

REPORTS OF THE SECTIONS

HERBARIUM SERVICES SECTION

The four herbaria of the Institute continued to identify plants and provide information for a wide range of people including officers of the Institute, various State and Provincial Departments, Universities and the public both in South Africa and its neighbouring states.

National Herbarium, Pretoria (PRE)

Mr E.G.H. Oliver, who administered the herbarium section for the past six years, has left Pretoria on transfer to Stellenbosch, where he is working intensively on Ericaceae. Mrs E. van Hoepen (acting curator) and Miss W.G. Welman (finances) have taken over the administration.

A total of 14 600 specimens was named and about 530 visitors were dealt with. 13 068 accessions were made to the herbarium. During the year 57 loans (7 484 specimens) were sent to other Institutes, and 35 loans (4 175 specimens) were received. PRE received 1 654 specimens on exchange, and sent out 1 190 duplicates during the year.

Numerous collecting expeditions were undertaken during the year, of which the more important were to the north-western Transvaal, an area which is poorly represented in PRE, northern Natal, the western O.F.S., north-eastern Cape and the Karoo, the south-western Cape, coastal areas of the southern and eastern Cape and Natal, and eastern Lesotho.

FIG. 1.— A group of dignitaries outside the CSIR Conference Centre, Pretoria, where the 10th AETFAT Congress was held in January 1982. Left to right: Prof. J. Miege, a former Secretary-General, Prof. J. Léonard, one of the founders and first Secretary-General of AETFAT, Prof. J.P.M. Brenan, President and former Secretary-General, Dr B. de Winter, Secretary-General (1979–1982), and behind, Dr P.H. Raven, keynote address speaker. Photo: F.N. Hepper.

The replacement of old herbarium cabinets by new modular steel cabinets continued. The old cabinets were sent to our units in Durban and Stellenbosch to replace old and unsuitable cabinets and provide much-needed expansion. To accommodate the rapidly expanding lichen collection eight cabinets of the type used for fossil collections have been temporarily placed in the western light well in the basement.

As regards visitors to the Herbarium, a record year was experienced, largely due to the AETFAT Congress. Many delegates took advantage of their visit to Pretoria to spend some time in the herbarium working on their particular interests. Among the overseas visitors were Prof. J.P.M. Brenan, ex-director of Kew; also from Kew came Dr W.D. Clayton and Mr F.N. Hepper; Drs E. Launert and N.K.B. Robson from the British Museum; Mr F. White from Oxford; Prof. K. Dahlgren from Copenhagen; Prof. and Dr O. Hedberg from Uppsala, Dr O. Almborn from Lund and Prof. R.B. Nordenstam from Stockholm; Dr I. Kukkonen from Helsinki; Prof. and Dr D. Müller-Doblies from Berlin (who spent several months in South Africa mostly collecting in the S.W. Cape), Prof. H.D. Ihlenfeldt and Dr H.E.K. Hartmann from Hamburg, who also spent extra time in the field on collecting, Prof. F. Weberling from Erbach, Prof. W. Rauh from Heidelberg; Prof. R.W. Wendelberger from Vienna; Dr A.J.M. Leeuwenberg and Dr D.O.W. Wijnands from Wageningen, Prof. M.J.A. Werger and Dr C.C. Berg from Utrecht, Dr F. van der Meulen from The Hague; Prof. J.E.J. Lambinon and Dr E. Serusiaux from Liège, Dr P. Bamps from Meise and Dr P. Goetghebeur from Gent; Dr P.H. Raven, Dr P. Goldblatt and Dr M.R.C. Crosby from Missouri Botanical Garden, St Louis; Prof. W.H. Eshbaugh from Oxford, Ohio; Drs R.B. Faden and A. Goldberg from the Smithsonian Institute, Washington, Prof. P.G. Mahlberg from Bloomington, Indiana and Dr H. Eichler from Canberra. From neighbouring states came Dr S. Talukdar and Mrs M.O. Schmitz (whose recent death was a great shock to all who knew her) from Roma, Lesotho; Mr E.N. Netshiungani from Venda and Mr O.H.D. Makunga from Fort Hare University.

Delegates to the Congress included botanists from all South African universities, Kirstenbosch, Nature Conservation and the Parks Board, many of whom made use of the herbarium while in Pretoria.

All of the herbarium staff were involved in some way or other with the AETFAT Congress and all spent a good deal of time preparing for the congress or helping assist or entertain the delegates. Identifications of specimens collected by our overseas visitors was completed as soon as possible. As a result a backlog of about four months of our normal work has built up, and we are very much in arrears with identifications.

Other visitors during the year included Dr Juliet Prior, from London who is doing archeological work in Swaziland, and Mrs E.S. Kemp from Mbabane, who is working on updating and expanding the Swaziland checklist.

Wing A: Mrs van Hoepen continued to control the wing in a part-time capacity, while also controlling the information and identification services.

Miss C. Reid is continuing her studies on the Cyperaceae including field work, and has done a great deal of curating and correcting of misidentifications.

Miss L. Smook has initiated a project in which eventually all the herbarium professional officers will participate, namely filling in gaps in our collections from under-collected areas. In this connection the computer has given valuable information and maps have been drawn up showing the number of collections per grid. She is also working on her booklet on the grasses of the Transvaal, and recording all common names of grassses she encounters.

Wing B: Mr G. Germishuizen, due to prolonged sick-leave following a serious operation, was not yet able to complete his project on Polygonaceae but should do so by the end of 1982. The book on Transvaal Wild Flowers with paintings by Mrs Fabian is nearing publication and Mr Germishuizen, who was responsible for the text, had to check the proofs. Another book for which he wrote the botanical descriptions, that of Dr Fox on Edible Plants, will also appear in print shortly.

Mrs L. du Toit gave valuable help in bringing Cythna Letty's Wild Flowers of the Transvaal up to date for the printing of a second edition. We were sorry to lose her when she resigned at the end of November. She has been replaced by Mrs P. Olivier. Mrs I.R. Leistner who also resigned has not yet been replaced.

The data bank encoders work in this wing and the spirit collection is also housed here.

Wing C: Miss E. Retief who is in control of this wing is continuing her studies of the Campanulaceae and is also assisting Mr P. Herman in his work on the identification of fruits and seeds. At the AETFAT Congress they jointly presented a poster paper on this subject.

Mr Herman is continuing work on this long-term carpological project, and has rounded off his work on *Pavetta.* He is responsible for most of the routine identification work in this wing.

Mrs M.J.A.W. Crosby who assisted with identifications in this wing was transferred to Wing D in January 1982.

During an overseas holiday tour Miss E. Retief paid visits to Edinburgh, Kew, Heidelberg and Genéve herbaria.

Wing D: Miss W.G. Welman, who controls this wing continues as regional extractor for Excerpta Botanica (Taxonomica) and has numerous administrative duties. A great deal of her time was spent in preparations for the AETFAT Congress. Among other duties she was responsible for the flowers used as decorations at the Congress and the "Meet and Greet" function at the start of the meeting. On the departure of Mr Oliver she is now responsible for the herbarium finances.

Mrs S.J. Smithies resigned in July 1981, and Mrs Crosby is now assisting with identifications in this wing.

Cryptogams: The departure of Dr R.E. Magill, who left in December 1981 for Missouri after completion of his contract left a gap in this section. Before leaving, however, he saw Bryophyta, part I, fasc. I in the Flora of Southern Africa series appear in print, and he is continuing his work on South African mosses, assisted by Mr J. van Rooy, who has taken over the Moss herbarium. Mr van Rooy recently obtained his B.Sc. degree.

Mr. F.A. Brusse has been working steadily at the lichen collection and spent four weeks on a field trip in the south-western Cape collecting for PRE. At present the lichens are housed under very cramped and unsatisfactory conditions in an open passageway, but we hope to have better accommodation within a few months.

Mrs S.M. Perold who assists with Bryophyte identifications and research, is also working on a Ricciaceae project. She operates the SEM in the examination of plant material for various taxonomists.

Mrs G.L. Radmacher, who was responsible for checking grid references, left the Institute in May 1981 to get married and is now living in W. Germany. Mrs I. Ebersohn who ran the service room (reception and sorting of incoming parcels, loans, listing of identifications, etc.) was transferred to the Administration section in January 1982 and has been replaced by Mrs M. Dednam.

Natal Herbarium, Durban (NH)

A total of 2 979 specimens was named, 499 visitors were dealt with as well as 6 student groups. Accessions to the herbarium numbered 1 698; 1 435 specimens were sent out on loan to various institutes.

Mr B.D. Schrire, the officer in charge of the unit, continued his studies of the Desmodieae, is working on the history of the Natal Herbarium and the collections housed therein with a view to its forthcoming centenary, and with the help of the Durban Parks department has done a major clean-up and reorganization in the garden.

Mrs B.J. Pienaar left the unit in June 1981 to take up duties in Pretoria in the Plant Exploration section and was replaced by Mrs M. Jordaan. Mrs C.E. Young who resigned in September 1981 was succeeded by Mrs M.K. Lynch and Mrs L. Nichols left at the end of February 1982.

In spite of this turnover of staff work at the unit is progressing smoothly, thanks to the organizing ability and leadership of Mr Schrire.

Albany Museum, Grahamstown (GRA)

A total of 1 979 specimens was identified and 847 visitors as well as 7 groups of students, totalling 99, was dealt with. Accessions to the herbarium numbered 1 108. 19 loans totalling 1 651 specimens were sent out and 463 donations of specimens were received, including 200 samples of kudu rumen.

Mrs E. Brink continues as officer in charge of the herbarium and information service, with the able assistance of Dr A.F.M.G. Jacot Guillarmod.

Seven displays were arranged in the museum foyer. The Grahamstown Nature Reserve, where encroachment by alien *Acacia, Hakea,* etc. is the main problem, was administered.

A start has been made in the moving of valuable plant specimens from the Albany Museum garden to the 1820 Settlers Wildflower Reserve to make way for the proposed extension to the Museum building due to start during the latter half of 1982. The herbarium will eventually be housed in the new extension and will have to be packed up during building operations, a major undertaking.

Government Herbarium, Stellenbosch (STE)

The number of specimens identified totalled 4 577; visitors numbered 388; accessions to the herbarium numbered 4 761 and 17 loans totalling 955 specimens were sent out.

Miss L. Hugo continues as curatrix of the herbarium. During February 1982 a number of AETFAT delegates were taken on a tour of the south-western Cape and as a result the herbarium dealt with a large number of identifications for these visitors.

Mrs C.M. van Wyk and Mrs A.C. Fellingham assisted with identifications and general herbarium work.

Mrs R.M. Wikner handled the technical aspects of the herbarium work with great efficiency.

Numerous collecting trips were undertaken and several flower shows were attended, where assistance was given in the identification of indigenous exhibits.

FLORA RESEARCH SECTION

The task of the section is to research into the taxonomy of the living and extinct plant species of Southern Africa, and to pass on the knowledge gained to expert and layman alike, mainly through publications.

Flora of Southern Africa

An international workshop session on the Flora was held during January with the aim of finding ways to speed up production of this work. The workshop was attended by 59 botanists. A drafting panel consisting of directors and senior researchers of leading biological research organizations in the United Kingdom, the United States of America, Sweden and South Africa reported on the results of the workshop to the congress of AETFAT and submitted a formal document to the Minister entitled the Flora of Southern Africa — a case for increased support for a research project of international scope and impact. *At a Plenary Meeting of AETFAT a resolution was passed unanimously in which delegates 'petition the Botanical Research Institute and the Government of the Republic of South Africa to take all possible steps to bring this vital project to a timely conclusion'.

During the AETFAT congress the state of progress of the project was demonstrated in a poster paper.

Two works were published during the year. The first is an introductory volume and the second a fascicle in the Cryptogam series. Both are discussed below.

Members of the Institute reported as follows on progress with research fascicles on volumes of the Flora:

Vol. 2: Register of names and types for Poaceae. Dr G.E. Gibbs Russell has completed this research facet. All names have been added to the Register from the Chase Index, Flora Capensis, Flora of Tropical Africa and various smaller accounts of southern African grasses. There are roughly 4 250 names in the Register, and it is expected that more will be added in the future. Poaceae—Meliceae. This facet was terminated by Dr G.E. Gibbs Russell during 1981 and the findings were accepted for publication in Bothalia.

Keys to Southern African grasses. Dr. G.E. Gibbs Russell sent draft copies of identification keys to genera and species, with information on recent synonymy, distribution and vegetative morphology for each species, to university departments of botany and pasture science for use and comments. The tribes Agrostideae, Andropogoneae, Bambuseae, Centosteceae, Maydeae, Meliceae, Olyreae, Oryzeae, Pappophoreae and Stipeae have been sent out. Arundineae, Ehrharteae and the first genera of Paniceae have also been completed.

Poaceae — Subfamilies Oryzoideae, Centostecoideae and Bambusoideae. In another research facet by Dr G.E. Gibbs Russell, all tribes have been studied in a preliminary way, provisional keys were written and species concepts formulated. The most difficult genus, *Ehrharta,* has been studied in detail and descriptions of two sections were written. Drawings of all genera have been completed except for the Bambuseae, which is dealt with by an outside collaborator.

Vol. 4: Xyridaceae, Eriocaulaceae, Commelinaceae, Pontederiaceae and Juncaceae. The facet was completed by Mrs A.A. Mauve. Only the genus *Aneilema,* which is being revised by an overseas researcher, is still outstanding. Parts of the manuscript were amended after discussions with experts from overseas.

Restionaceae. A checklist by Dr H.P. Linder of the Southern African Restionaceae has almost been completed in consultation with Miss E. Esterhuysen of the Bolus Herbarium of the University of Cape Town. This list presents initial hypotheses on supra-specific groups, indicates problem species and species aggregates, and includes all new species. It thus provides the framework on which the remainder of the taxonomic work on the group will be done. Study of seeds and pollen has been commenced with the aid of the scanning electron microscope. First results indicate that taxonomically important information can be expected from this study.

Vol. 5: Liliaceae — Dracaenoideae and Asparagoideae. A revision of the genus *Asparagus* published in 1966 is being updated and adapted to the Flora format by Mrs A.A. Mauve. A few new species have been recognized. There appears to be a taxonomically important correlation betwen the inflorescence type and the root system.

Vol. 7: Iridaceae. Editing of the fascicle on *Syringodea* and *Romulea* by Prof. M.P. de Vos of the Universtiy of Stellenbosch was completed.

Vol. 8: Orchidaceae — Disinae. Studies on the systematics of the Disinae have been completed by Dr H.P. Linder. Various publications on the group have been published in journals both in South Africa and overseas. Information on the phytogeography of the Disinae was presented at the AETFAT congress. Two workshops were held on the cladistic classification techniques employed in the project.

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* The drafting panel of this document consisted of: Prof. J.P.M. Brenan, Dr B. de Winter, Prof. O. Hedberg, Dr E. Launert, Dr O.A. Leistner and Dr P.H. Raven.

Vol. 11: Mesembryanthemaceae — Ruschiinae. Dr H.F. Glen investigated microscopic seed characters of about 100 species. He took colour microfilm photographs of all types of Ruschiinae at Kew and assigned most of the unidentified material of that group at Kew to previously known taxa. Cytological investigations proved taxonomically unfruitful.

Vol. 18: Burseraceae. An account of the genus *Commiphora* by Prof. J.J.A. van der Walt of the University of Stellenbosch is being edited.

Vol. 21: Tiliaceae. The completed manuscript of this family is being updated by Dr L.E. Codd.

Vol. 25: Ericaceae. Two new species were described in the genera *Erica* and *Scyphogyne* by Mr E.G.H. Oliver.

Vol. 28: Lamiaceae. Thirteen genera (including *Salvia* and *Stachys*) totalling 95 species, which had been revised previously by Dr L.E. Codd, were rewritten by him in the new format. He also revised and wrote up seven genera with a total of 28 species. A display of live plants of the genus *Plectranthus* was held at Kirstenbosch during February to demonstrate the horticultural value of this group. More than 30 species, with many cultivars, were exhibited.

Vol. 30: Acanthaceae — *Justicia*. Miss K.L. Immelman investigated all collections from the National Herbarium, Pretoria and about half the collections from other South African herbaria. The information has been taken up in a card index. Preliminary distribution maps, descriptions and a key to species have been drawn up.

Vol. 33: Asteraceae — Gnaphaliinae. A manuscript by Prof. O.M. Hilliard of the University of Natal, dealing with 330 species, has been edited in parts and will go to the printer soon.

Cryptogams — Algae. A checklist of macrophytic marine algae by Prof. S.C. Seagrief of Rhodes University is being prepared for publication.

Cryptogams — Bryophyta. Part 1, fascicle 1 of this work, which deals with 190 species of mosses of the families Sphagnaceae to Grimmiaceae, prepared by Dr R.E. Magill and Mr J. van Rooy, was published. The work includes 83, mostly full-page, plates of very detailed pencil drawings and 110 distribution maps. The introduction gives hints on collecting and identification of mosses and includes a comprehensive illustrated glossary. The manuscript for the major part of fascicle 2 has been received. Work is proceeding on the rest of fascicles 2 and 3.

Cryptogams — Pteridophyta. Text of 38 species of several families such as Polypodiaceae was received from Prof. E.A. Schelpe of the Bolus Herbarium of the University of Cape Town. Editing of 180 species previously received was largely completed.

Botanical exploration of Southern Africa

A book with this title written by Miss M.D. Gunn and Dr L.E. Codd, was published for the Institute by A.A. Balkema. The work consists of two sections. The first gives an historical outline of the expeditions, collecting and publications concerning South African plants up to the middle of the 18th century. The second section is a dictionary of plant collectors comprising some 3 300 entries of which about half are provided with biographical notes. The book has 400 pages and includes 81 reproductions of old botanical pictures and maps and 440 portraits.

Ceropegia *and related genera*

The first printers' proofs of this semi-popular treatise by Dr R.A. Dyer on the genera *Ceropegia, Riocreuxia* and *Brachystelma* have been corrected and returned. The book is being published for the Institute by A.A. Balkema.

Register of plant taxonomic projects

The latest edition of this work has been prepared for publication in the forthcoming volume of the AETFAT Bulletin.

Pretoria Flora

Camera-ready copy of 52 of the projected 750 pages of this work was completed. It includes identification keys and text of the families Cyperaceae, Liliaceae and Euphorbiaceae. Text of a further 384 species belonging to the ferns and 45 families of flowering plants was typed. Some of the larger families included are Aizoaceae, Apiaceae and Verbenaceae.

Palaeoflora of Southern Africa

Camera-ready copy of the revision of the genus *Dicroidium,* which is undertaken by Drs J. and H. Anderson, has been completed. It comprises 78 one-colour pages, 40 pages with two-colour line illustrations and 110 pages with black/white photographic plates. The work is to be published by the private sector.

Liaison officer, Kew

The present incumbent, Dr H. Glen, continued to provide information concerning mainly the taxonomy and nomenclature of southern African plants to the Institute and to other botanical research centres in South Africa and overseas. He also assisted in the mounting of an exhibition of botanical art by Cythna Letty, formerly of this Institute, at the galleries of the Royal Horticultural Society in London. For this exhibition she was awarded the Grenfell silver-gilt medal of the Society. Research work by the liaison officer was directed mainly towards numerical taxonomy of the Mesembryanthemaceae.

Herbarium activities — PRECIS

PRECIS, the computerized data base of the National Herbarium, was restructured by Dr R.E. Magill and Dr G.E. Gibbs Russell, to make its operation more economical and flexible. The system was reduced in size by converting it to a strictly specimen-based data bank. All ecological and economic data was eliminated. Grid references have now been inserted on about 330 000 of the specimens in the base and the system is now in active operation.

PLANT STRUCTURE AND FUNCTION SECTION

The year under review has been very productive and stimulating with good progress being made on all the research projects of the section. There have been no staff changes and all projects have advanced to the stage where results will soon be forthcoming.

Comparative grass leaf anatomy

Dr R.P. Ellis has focused his attention on studies of bamboo leaf anatomy during the past year. Anatomical material of over 200 species has been acquired and examined. Represented in this sample are world-wide collections of all the tribes of the bambusoid subfamily collected mainly in Central and South America and Asia. These studies have been undertaken in conjunction with the Smithsonian Institution in Washington and have resulted in a revision of the indigenous South African bamboo — *Arundinaria tessellata.* The co-operative work on the taxonomy and anatomy of the Bambusoideae is being continued.

The anatomy of the South African representatives of genera such as *Panicum, Alloteropsis, Echinochloa, Eragrostis* and *Leptochloa* has also been concentrated on with the SEM helping considerably in the case of *Leptochloa.* Anatomical indications are that in all these genera, taxonomic problems exist. Collecting expeditions to the Caprivi Zipfel and Natal should help provide convincing anatomical evidence to prove that revisions of all these genera are needed.

Grass identification by epidermal structure for herbivore food preference studies

The objective of Mrs R. Botha's research project is the quantification of plant material, in the diet of grazing herbivores. Three grass species are initially being studied viz. *Themeda triandra, Eragrostis capensis* and *Brachiaria serrata.* Preliminary results indicate no clear intraspecific differences between the leaf blades and sheaths of grasses from different geographical areas as regards epidermal anatomical characteristics. Intraspecific differences have been observed between the laminas and sheaths of the species studied. Allowance for these differences must be made in the microscopic identification of grass fragments in rumen or faecal analysis. *In vitro* digestion studies at this stage indicate no clear differences between specimens of the same grass species collected from different areas but these studies have shown that sheaths are consistently less digestible than the leaf blades.

In a preliminary microscopic investigation of impala rumen samples from Loskop Dam Nature Reserve it was observed that *Panicum maximum* constituted the most important grass species in their diet.

Cytogenetic studies

Embryo sac studies of several species, such as *Lantana camara, Rubus* and *Anthephora pubescens* are being undertaken by Mr J.J. Spies to determine the degree of sexuality in these species complexes. It has been shown that *Lantana camara* only reproduces sexually and that sometimes two sexual embryo sacs per ovule are formed. Meiotic data on *Lantana camara* are being analysed by computer in order to try and establish relationships in this complex.

In addition various crosses between different sorghums are being made in an attempt to determine relationships in the genus *Sorghum.* An intergeneric hybrid between *Aloe* and *Bulbine* is also being studied cytogenetically.

ECOLOGY SECTION

Transvaal bushveld studies

A pilot study on the Sour Bushveld (Veld type 20) has been completed by Mr R.H. Westfall who has submitted his final report. The vegetation has been classified and mapped. Plant communities were subjected to ordination to determine environmental gradients and layer diagrams were used to illustrate community structure. Suggestions for the application of veld-condition assessments in respect of grazing potential in bushveld vegetation include the use of the quadrat method with the Domin-Krajina cover-abundance scale for estimating canopy cover.

Transvaal forest survey

The field work on the lower section of the transect study of the Sabie area has been completed by Mr G.B. Deall, who is preparing the data for processing. The usefulness of the land-type map for stratification of the area for stratified random sampling will also be assessed.

Coastal studies

Dr P.J. Weisser has completed his tabulation of the field data of the Mlalazi Estuary-Richards Bay dune area. Twenty-two mapping units have been established and described, fourteen vegetation maps (scale 1: 10 000) drawn and twenty-five pages of manuscript completed. The vegetation changes of part of the future Kwazulu Botanical Garden were monitored and quantified using aerial photographs. When protected, the dune vegetation recovers rapidly. The aquatic, semi-aquatic and adjoining terrestrial vegetation of 38 Cape estuaries was studied and mapped by Miss R.J. Parsons using air-photo and field data. For eight estuaries the information has been published in CSIR reports.

Literature search reveals a dearth of botanical information on Cape estuaries. In most situations studied, the vegetation is badly degraded or is threatened, owing mainly to overexploitation or other mismanagement.

Cape fynbos studies

(a) *Vegetation survey of the Cape of Good Hope Nature Reserve*

Reports on this survey are being prepared by Mr H.C. Taylor as papers for publication. From the results of the trial of methods reported in the first paper it is concluded that, with the type of sampling used, the synthetic phytosociological Braun-Blanquet method provides a more natural classification of communities of the Reserve than does the monothetic, divisive association-analysis method. In the second paper the habitat and vegetation of the Reserve are described. Ten fynbos and two scrub-forest communities are recognized.

(b) *The vegetation of Swartboskloof, Jonkershoek*

Mr D.J. McDonald is making good progress on a semi-detailed study of the fynbos and forest communities of the Swartboskloof catchment. This area is the Fynbos Biome Project's Mountain Fynbos intensive study site. Phytosociological approach and methods are being used for this survey and to date 158 plots have been sampled. Data from 97 sample plots have been edited, coded and placed on computer file for processing. Preliminary phytosociological tabulation is well advanced.

(c) *A study of the vegetation along transects through the Western Cape forelands*

Mr C. Boucher has distinguished and mapped (at a scale of 1: 10 000) nine plant communities, representing subdivisions of two veld types, namely West Coast Strandveld (Veld Type 34) and Coastal Fynbos (Veld Type 47), at the Fynbos Biome Project's Coastal Fynbos intensive study site near Pella, Atlantis.

A preliminary check-list of flowering plants and ferns has been compiled. The check-list includes information about the periodicity of the 402 species collected in this 269 ha site. Seven species recorded here were found to be listed in the threatened plants of southern Africa report.

Four major vegetation units have been identified in the western forelands from the analysis of 338 sample plots and 778 species. The three veld types, West Coast Strandveld, Coastal Renosterveld and Coastal Fynbos, have now been defined more accurately while an additional category of wetland vegetation must still be described.

The Coastal Renosterveld was found to be closely related to Mountain Fynbos vegetation found on clay-rich soils, together with inclusions of West Coast Strandveld vegetation in specific habitats. Coastal Renosterveld was deduced to be the product of a recent history of regular disturbance through a short-interval burning régime, overgrazing and ploughing.

Aquatic ecology

An ecophysiological study of water hyacinth in Natal

The report by Mr C.F. Musil on the kinetics of nitrogen- and phosphorus- limited growth rates of *Eichhornia crassipes* in the laboratory and in the field has been revised and rewritten. Growth rates of *E. crassipes* in the field have been shown to be fairly accurately predicted from the nitrogen and phosphorus growth-rate limiting concentrations in the water and from those in the plant tissues, using a refined predictive model generated as a result of this investigation. Mr Musil has demonstrated the manner in which the refined predictive model can be used to calculate yields, growth rates and amounts and frequencies of harvest for *E. crassipes* growing in polluted waters to control nutrient enrichment, as well as excessive growth of this plant.

Ecological literature indexing

An ecological bibliography for southern Africa is currently being compiled, especially by Mrs A.J. Engelbrecht and Mr R.H. Westfall. References recorded by researchers at the Botanical Research Institute are being expanded and incorporated into a computer data base. All references are being annotated with codes, key words, biomes and regions where applicable. The IBM/STAIRS programme package is used for retrieving references by means of author and subject headings as well as by alphabetical sorting.

National Conservation Plan

Since a full-time co-ordinator and staff for the NAKOR National Plan for Nature Conservation are now being provided by the Department of Environment Affairs, the co-ordination and data-processing services rendered on a part-time basis by the Ecology Section are being transferred to that Department. The data base has begun to firm sufficiently to provide a more solid basis for scientific conservation planning.

PLANT EXPLORATION SECTION

During 1980/81 it was decided that the section's weed research activities should be phased out in favour of plant utilization research.

This year the process was taken a step further with the decision that we should further concentrate our efforts on food plants, phasing out work on other facets such as barrier plants and wood utilization. Mr M.J. Wells the head of the section is personally supervising the rounding off of facets that are being phased out, whilst Mr T.H. Arnold is leading the research on food plants.

Conservation of germ plasm

Mrs K.J. Musil reports that seed collections of primitive crops (mainly forms of *Sorghum, Pennisetum, Citrullus* and *Lagenaria*) numbered 576. Some material went to the germ plasm bank for future breeding programmes, the rest being retained for research on crop diversity.

Eighty-eight black families were interviewed regarding crop preferences, to establish which crops are liable to be lost. Factors determining preferences range from diversity of use to susceptibility to bird and insect attack. Traditional grain crops are losing ground to modern maize cultivars, and there is little concern, at local level, for their conservation.

Crop diversity: origin and classification of sorghum

As a result of Mr Arnold's work all five races of primitive crop sorghums (*Bicolor, Guinea, Caffra, Caudatum* and *Durra*) have now been recorded from South Africa, typical forms of the latter two races being recorded for the first time. Seven intermediate races have also been recorded, collectively exhibiting an almost continuous range of variation, and constituting an important source of germ plasm.

A new taxonomic character, a zone of weakness and groove which facilitate separation of the grain at threshing, has selective advantages. Its differentiation provides new evidence regarding the evolution and movement of sorghum races in Africa.

This project is in co-operation with the Summergrain centre and the Sorghum Beer Research Institute, CSIR.

Crop diversity: other primitive crops

Primitive forms of six other crops of African orgin (*Pennisetum americanum, Vigna unguiculata, Voandzeia subterranea, Citrullus lanatus, Lagenaria siceraria* and *Hibiscus esculentus*) and four of extra-African origin (*Zea mays, Arachis hypogaea, Cucurbita pepo* and *Phaseolus radiatus*) were collected by Mr Arnold and Mrs Musil for investigation. Of these only *Hibiscus* and *Phaseolus* showed little variability. The other crops were very variable. *Vigna unguiculata* (cowpea) variants with cream, beige, orange, red, mauve, purple and black fruits, either plain or speckled, kidney-shaped or diminutive and angular, were found. Crop diversity studies are continuing.

Tribal plant uses

A study of ethno-botany in southern Africa as reflected in publications, unpublished manuscripts, museum and herbarium holding (including over 300 references) was completed by Miss C.A. Liengme. The state of knowledge was reviewed in terms of each tribal group and each plant use. It was found that relatively little is known of plant use by the Swazi, Transvaal Ndebele, Mpukushu (of the Okanvango Delta) and the Khoi. Food and medicinal uses have received most attention whilst the many and diverse uses of woods are least well documented.

Food plant list

A start has been made with the compilation of a National Food Plant List, along the same lines as the National Weed List. To date the list includes the names of 985 edible, indigenous plants, culled from ethno-botanical and other literature by Mrs Musil and Miss Liengme.

Wood use by the Tsonga

In a study area covering 18 000 hectares and housing 978 Tsonga families in Gazankulu it was found that firewood use averaged 15 kg per family per day (5 300 tons p.a. for the whole area). This consisted almost entirely of dead wood. The demand for building timber totalled only 28 tons p.a. but accounted for many living trees. Both firewood collection and timber cutting for hut-building were highly selective with a few species such as *Colophospermum mopane* providing almost all the wood. This study is now being written up by Miss Liengme.

Tree distribution in the Transvaal

Dr John Anderson reports that most of the field work has been completed, and the accent this year was towards plotting field distribution data, preparation of a leaf catalogue, and line drawings for each species.

A high proportion of the distribution data has now been plotted on a set of draft maps. This work was continued by Miss A. Jooste and 200 A4 cards, with leaf-vouchers, supporting the field observation data, have been prepared. Line drawings of 263 of the woody species have been completed by Ms J. van Gogh.

Field data has been contributed in the SE Transvaal (10 1/16 degree square units) by Mr P. Venter and in the NE Transvaal (15 units) by Mr M. Amm.

Barrier plants

An exploratory survey of potential barrier plants has been completed and is being written up by Miss L. Henderson. The literature survey yielded the names of 294 exotic species and 120 indigenous species that have been used as barrier plants in South Africa. To this list have been added the names of a further 180 indigenous species with potential as barrier plants. They have been classified as decorative hedges, windbreaks or security hedges and data forms have been completed for 70 recommended species.

Scientific information service

The Institute's head office in Pretoria received 1 658 visitors seeking information. Of these 730 visited the herbarium, 310 the data section, 310 ecology, 203 the library, 71 plant exploration, 20 structure and function, 19 flora and 279 unspecified. Our Scientific Information Officer, Mrs D.M.C. Fourie assisted by Mrs B.J. Pienaar, dealt with 22 visitors, 138 telephonic enquiries, 334 postal enquiries and identified 250 cultivated plants. The most substantial reports produced on request were on the status of *Prosopis* in South Africa, and a bibliography of references on aquatic and terrestrial plant invaders.

Educational information service

The educational service run by Mrs B.J. Pienaar hosted 21 groups of scholars or students and 16 adult groups: a total of 1 556 visitors. Regular foyer exhibits were prepared, including named thematic exhibits of flowering or fruiting material from the garden. An up-to-date brochure on the Institute was prepared, and 17 radio talks on Institute activities were organized.

A highlight was the visit of many prominent overseas botanists attending the AETFAT Congress. Many returned to make use of our research collections and expressed great appreciation of the work done and the facilities available.

Photographic collection

Over 5 000 colour slides and 1 500 black and white prints and negatives were acquired from the estate of the late Mr Hans-Joachim Schlieben, a noted plant collector. They include coverage of Madagascar, the Comoro Islands, the Mascarenes, Seychelles and southern Africa, as well as an historic collection of black and white slides of an expedition to Mt Kiliminjaro in 1933. Mr A.A. Balsinhas has annotated and filed most of the collection.

National weed list

Mrs V.M. Engelbrecht who is on the staff of the Plant Protection Research Institute, but seconded to us, completed data sheets for all listed species. She also completed 75% of the weed family summaries and prepared an index. Analysis of the weed data revealed: a few large plant families provide over 50% of our weeds; Monocotyledons are twice as likely to be weeds as are Dicotyledons; exotic weeds are more versatile than indigenous species in their home environment; the major invasive weed groupings are herbs from Europe and Asia and trees from Australia but South America probably has the greatest potential to provide us with new weeds. This and other data was presented in three papers to AETFAT.

Lantana camara

A total of 51 variants belonging to five colour races of *Lantana camara* have been described and photographed by Mr C.H. Stirton but it is clear that many other variants exist, and that we are dealing with a hybrid swarm. Collecting and cytogenetic evaluation of the material is continuing, but no further variants are being described until those already described have been screened for susceptibility to biological control agents. Mr Stirton has prepared several papers in conjunction with Mr J.J. Spies who is handling the cyto-genetic aspects. Mr Stirton has now left our service and the *Lantana* facet is being completed by Mr Spies of the Structure and Function Section.

Woody invaders

Miss Henderson and Mrs Musil have now sampled a total of 54% of the quarter degree squares in the Transvaal (12% this year) for exotic woody invaders. The number of invader species recorded has risen to 53, of which five were recorded for the first time this year.

BOTANICAL GARDEN

The garden is still without a curator, and Mr H.J. de Villiers (garden) and Mr D.S. Hardy (nursery) continued in charge of their respective sections.

The garden records section consisting of Mrs B.C. de Wet, Mrs K.P. Clarke and Miss K. Behr handled 1 580 accessions, including 750 general research collections and 830 experimental collections.

A large part of the unique collection of Madagascan plants built up by Mr Hardy was successfully transferred to a newly roofed shade house, whilst the main display house was renovated. Landscaping of the Karoo biome area and the water garden in the general planting area continued under the direction of Mr de Villiers.

The garden and the Institute suffered a very sad loss on 5 January 1982 with the death of Mr Jan Erens. He was the first horticulturalist associated with the establishment of the garden under Dr R.A. Dyer. At the time of his death he was responsible for the mass propagation of plants for display purposes.

BOTANICAL RESEARCH INSTITUTE

Scientific, Technical and Administrative Staff

(31st March 1982)

Director

B. de Winter, M.Sc., D.Sc. (Taxonomy of Poaceae, especially *Eragrostis* and of *Hermannia;* plant geography)

Deputy Director

D. J. B. Killick, M.Sc., Ph.D., F.L.S. (General taxonomy, nomenclature, mountain ecology and editing)

Assistant Director

(Agricultural Research Leader)

D. Edwards, M.Sc., Ph.D. (Ecological methodology, aquatic plants, remote sensing, vegetation structure and physiognomy)

ADMINISTRATION

Administrative Officer....	D. F. M. Venter
Senior Administrative Assistant..................	Mrs D. J. Gerber
Senior Administrative Assistant..................	Mrs J. M. Mulvenna
Administrative Assistants	Miss H. M. Schreüder Mrs J. J. van Niekerk
Personal Secretary to Director	Mrs M. M. Loots
Senior Clerical Assistant	Mrs T. Creffield (Registry)
Clerical Assistants..........	Mrs C. A. Bester* Mrs C. van Niekerk* Mrs I. J. Joubert* (Registry)
Receptionist	Mrs I. Ebersohn
Typists	Mrs S. S. Brink Mrs J. Gerke* Mrs S. M. Thiart* Mrs M. P. M. C. v.d. Merwe*
Technician: Assistant to Secretary-General: AETFAT................	Mrs B. A. Momberg, B.Sc.*

HERBARIUM SERVICES SECTION

Officer in Charge...........	E. G. H. Oliver, M.Sc., (until January, 1982)
Officer in Charge (Acting)	Mrs E. van Hoepen, M.Sc. (from February, 1982)

NATIONAL HERBARIUM, PRETORIA (PRE)

Agricultural Researchers	E. G. H. Oliver, M.Sc. (Curator; Ericaceae) (until Jan. 1982) Mrs E. van Hoepen, M.Sc. (Curator; supervision of identifications and enquiries)
Senior Administrative Assistant..................	Mrs J. Mulvenna

Wing A (Cryptogams – Monocotyledons)

Agricultural Researchers	Mrs E. van Hoepen (until January, 1982) Miss C. Reid, B.Sc. Hons (Cyperaceae)
Research Technician	Miss L. Smook, B.Sc. (Poaceae)
Technical Assistant	Mrs A. M. Fourie*

Wing B (Piperaceae – Oxalidaceae)

Agricultural Reseachers	G. Germishuizen, B.Sc. Hons (Polygonaceae) Mrs L. du Toit, B.Sc. Hons (until December, 1981) Mrs P. Olivier, B.Sc. Hons (from January, 1982)
Technical Assistant	Mrs I. R. Leistner* (until December, 1981)

Wing C (Linaceae – Asclepiadaceae)

Agricultural Researchers	Miss E. Retief, M.Sc. (Campanulaceae) P. P. J. Herman, B.Sc. Hons
Research Technician	Mrs M. J. A. W. Crosby, B.Sc.* (until December, 1981)
Technical Assistant	Mrs J. I. M. Grobler*

Wing D (Convolvulaceae – Asteraceae)

Agricultural Researchers	Miss W. G. Welman, M.Sc.
Research Technician	Mrs M. J. A. W. Crosby, B.Sc.* (from January, 1982)
Technical Assistant	Mrs W. le Grange* (until August, 1981) Mrs S. S. Human (from March 1982)

Cryptogamic Herbarium

Agricultural Researchers	R. E. Magill, M.S., Ph.D. (Musci) (until December 1981) F. A. Brusse, M.Sc. (Lichens)

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*Half-day.

Technical Assistants	J. van Rooy (Musci) Mrs L. R. Filter* Mrs P. W. van der Helde

Services

Research Technician	Mrs S. M. Perold, B.Sc.* (S.E.M. and laboratory work)
Technical Assistants	Mrs I. Ebersohn (Herbarium records, loans and exchanges etc) (until December 1982) Mrs M. Dednam* (Herbarium records, loans and exchanges etc) (from March 1982) Mrs G. L. Radmacher (Grid references and phytogeography) (until May 1981) Miss D. Frost (stationed at Bolus Herbarium) (until Feb. 82) A. Linder* (stationed at Bolus Herbarium) (until June 1981)
Typist	Mrs A. M. Verhoef
Laboratory Assistants.....	J. Phahla (Mounting) W. Kgaditsi (Preparation and packing) (until December 1981) G. Lephaka (Preparation and packing) (from January 1982)

Data Bank

Technical Assistant	Mrs J. H. Jooste

Photographic Room

Photographer................	Mrs A. J. Romanowski

NATAL HERBARIUM, DURBAN (NH)

Agricultural Researcher	B. D. Schrire, B.Sc. Hons (Curator; Fabaceae and general identifications)
Research Technician	Mrs M. Jordan, B.Sc.* (from June 1981) Mrs B. J. Pienaar, B.Sc. (until June 1981)
Technical Assistant	Mrs L. Nichols, Dipl. Art (until March, 1982)
Clerical Assistants..........	Mrs C. E. Young* (until June, 1981) Mrs M. K. Lynch* (from October, 1981)
Laboratory Assistant	C. Buthelezi

ALBANY MUSEUM HERBARIUM, GRAHAMSTOWN (GRA)

Agricultural Researchers	Mrs E. Brink, B.Sc. (Curator; general identifications) Mrs A. F. M. G. Jacot Guillarmod M.A., M.Sc., D.Sc.*
Technical Assistant	Miss G. V. Britten*
Laboratory Assistant	A. Booi

GOVERNMENT HERBARIUM, STELLENBOSCH (STE)

Agricultural Researchers	Miss L. Hugo, M.Sc. (Curator; general identifications) Mrs C. M. van Wyk, M.Sc.
Research Technician	Mrs A. C. Fellingham, B.Sc.
Technical Assistants	Mrs R. Wikner Mrs W. J. Geldenhuys (from February, 1982)
Clerical Assistant...........	Miss E. N. Pare
Laboratory Assistant	J. Ambraal

FLORA RESEARCH SECTION

Officer in Charge	O. A. Leistner, M.Sc., D.Sc., F.L.S.

FLORA OF SOUTHERN AFRICA TEAM

Research Leader	O. A. Leistner, M.Sc., D.Sc., F.L.S. (General taxonomy)
Agricultural Researchers	E. G. H. Oliver, M.Sc. (Taxonomy of Ericaceae) J. M. Anderson, M.Sc., Ph.D. (Palaeobotony, plantgeography) H. F. Glen, M.Sc., Ph.D., F.L.S. (Numerical taxonomy, Mesembryanthemaceae) Mrs G. E. Gibbs Russell, B.S., Ph.D. (Taxonomy, especially grasses; computerized data processing) Miss K. L. Immelman, M.Sc. (Taxonomy, especially *Justicia)* H. P. Linder, B.Sc., Ph.D. (Taxonomy, especially Orchidaceae and Restionaceae)

	L. E. W. Codd, M.Sc., D.Sc. (Taxonomy, especially Lamiaceae; history of plant collecting)
	Mrs A. A. Mauve, M.Sc. (Taxonomy, especially Monocotyledons)
Research Technician	Mrs H. M. Anderson, M.Sc., Ph.D.* (Palaeobotony)
Graphic Artists	Mrs R. C. Holcroft*
	Miss C. E. Smith B.A.*
Technical Assistant	Mrs C. F. Fourie

PLANT STRUCTURE AND FUNCTION SECTION

Agricultural Researcher	Dr R. P. Ellis, M.Sc., D.Sc. (Anatomy of South African grasses)
Agricultural Researcher	Mr J. J. Spies, M.Sc. (Cytogenetics of *Lantana* and *Sorghum*)
Agricultural Researcher	Mrs R. Botha, B.Sc., Hons (Applied grass anatomy studies)
Research Technician	Mrs I. Helberg, B.Sc., H.E.D. (Cytogenetics)
Technical Assistant	Miss H. Botha (Microtechnique)
Learner Technician	Miss A. Alberts

ECOLOGY SECTION

Officer-in-Charge	J. C. Scheepers, M.Sc., D.Sc.

REGIONAL STUDIES

Agricultural Research Leader	J. C. Scheepers, M.Sc., D.Sc. (Vegetation ecology, especially of forest/woodland/grassland relationships; conservation and land-use planning; phytogeography)
Agricultural Researchers	C. Boucher, M.Sc. (Lowland fynbos ecology and phytosociology; conservation and land-use planning; Braun-Blanquet approach and techniques)
	G. B. Deall, B.Sc. Hons (Vegetation ecology of forest/woodland/grassland interrelationships)
	D. J. McDonald, B.Sc. Hons (Mountain fynbos ecology and phytosociology; Braun-Blanquet approach and techniques)
	C. F. Musil, M.Sc. (Aquatic ecology and survey of aquatic plants, especially in Natal; ecophysiological studies on *Eichhornia crassipes* and *Salvinia molesta)*
	H. C. Taylor, M.Sc. (O/C Botanical Research Unit, Stellenbosch; mountain fynbos and forest ecology; Braun-Blanquet approach and techniques; conservation)
	R. H. Westfall, M.Sc. (Ecology and Phytosociology of Transvaal Bushveld)
Research Technicians	Mrs A. J. Engelbrecht, B.Sc. (Ecological data processing and presentation; ecological literature; nature conservation; air-photo interpretation and cartography)
	Mrs J. Schaap, H.P.E.D. (Draughtsmanship and cartography; artwork, layout and design)
	Miss A. P. Backer, B.Sc. (Ecological data processing and presentation; ecological literature; nature conservation; air-photo interpretation and cartography)
Research Technician	Mrs H. M. Cochrane, B.Sc. Hons* (Ecological literature; librarianship; conservation)

ENVIRONMENTAL ECOLOGY

Agricultural Researchers	P. J. Weisser, Ph.D. (Reedswamp ecology; ecological planning and environmental impact studies; Zululand coast dune vegetation; conservation)

	M. G. O'Callaghan, B.Sc. Hons (Estuarine ecology and phytosociology)
Research Technician	Miss E. C. A. Smith, B.Sc. (Ecological planning and environmental studies; conservation)
Technical Assistant	C. K. Roxburgh (Applied ecology and environmental studies)

EXPERIMENTAL ECOLOGY

Agricultural Researchers	M. C. Rutherford, M.Sc., Ph.D., Dipl. Datamet. (Biomass and production studies in woodland and fynbos ecosystems; competition and stress in fynbos ecosystems) Miss F. M. Pressinger, B.Sc. Hons (Ecophysiological studies in fynbos; competition and stress in fynbos ecosystems)

PLANT EXPLORATION SECTION

Officer in Charge	M. J. Wells M.Sc.
Research Leader	M. J. Wells M.Sc. (Weed Research, palaeo-ethnobotany, botanical horticulture, fynbos utilization and conservation)
Agricultural Researcher	T. H. Arnold, M.Sc. (Primitive crop plants, particularly *Sorghum*) C. A. Liengme, B.Sc. Hons (Ethnobotany, wood use) K.J. Musil, B.Sc. Hons (Conservation of Germ plasm and primitive crops) L. Henderson B.Sc. Hons (Clover and barrier plants)
Research Technicians	D. M. C. Fourie B.Sc. (Scientific information service and identification of exotics) V. M. Engelbrecht B.Sc. (Weed Research) † B. J. Pienaar B.Sc. (Public relations and identification of exotics)

	A. A. Balsinhas (Plant collecting, slide collection)
Clerical Assistant	N. Nigrini (Sectional Administration)

PRETORIA NATIONAL BOTANICAL GARDEN

Curator	Vacant
Acting Curator (garden)	H. J. de Villiers
Acting Curator (nursery)	D. S. Hardy
First Research Technicians	D. S. Hardy (Nursery supervision, succulents and orchids) H. J. de Villiers NTC III (Hort.) Dipl. Rec. P.A. (Development of savanna biomes and coastal forest)
Senior Research Technician	T. A. Ankiewicz, Dip. For. (Workshop & technical services, grounds and buildings)
Research Technician	K. Behr (Garden utilization, development of Fynbos Biome)
Technical Assistant	J. Taussig
Learner Technicians	P. van Eeden A. M. Cilliers K. Kruger
Technical Assistants	B. C. de Wet B.A.* (Garden records) K. P. Clarke (Garden records)
Farm Foreman	G. J. Stolz H. N. J. de Beer
TN 4 Supervisor	L. C. Steenkamp
TN 6	J. P. Booysen

PUBLICATIONS BY THE STAFF
(1 April 1981 - 31 March 1982)

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†Plant Protection Research Institute, Pretoria.

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WEISSER, P.J. & DREWS, B.K., 1980. List of vascular plants of the forested dunes of Maputaland. In M.N. Bruton & K.H. Cooper, *Studies on the ecology of Maputaland* 91–101. Grahamstown: Rhodes University and Natal Branch of the Wildlife Society of Southern Africa.

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Book Reviews

Trees and Shrubs of the Etosha National Park by Cornelia Berry with illustrations by Blythe Loutit. *Windhoek: Directorate of Nature Conservation.* 1982. Pp. 161, 50 line drawings, 14 full colour plates. Also available in German. Price R7,95.

This small, soft-covered book is an informative field guide to trees and shrubs of the Etosha National Park in South West Africa/Namibia. Such a guide is long overdue. The book is chiefly the work of two women: Cornelia Berry, wife of the biologist at Etosha, who did the research and wrote the text and Blythe Loutit, wife of a nature conservator, who was responsible for the illustrations.

Brief and simplified descriptions of the nine major vegetation types found in the Park are provided and their location is shown on the map of the Park which appears in front of the guide. Following this are descriptions of 53 trees and shrubs, the species being listed alphabetically according to their scientific names. The descriptions include brief details of the bark, thorns, leaves, inflorescences, flowers and fruit. Characters which are regarded as particularly diagnostic fall under the heading of 'Characteristic' printed in bold. If two or more species are considered difficult to distinguish from each other, the points of difference are compared in tabular form. Also included under each species is information on habit, distribution, nutritional value to the fauna and avifauna of the Park, as well as medicinal uses. Vernacular names in English, Afrikaans, German and Herero are given when available.

Each tree and shrub is illustrated by a simple black and white line drawing showing the main features of the plant. In the manner of Dick Findlay, Blythe Loutit has provided a background picture to each botanical drawing, for example various animals appearing in typical veld scenes. Fourteen full colour plates of some of the more important trees complete the illustrations.

A most useful feature of the guide are the lists of plants commonly occurring in the three tourist camps, Okaukuego, Halali and Namutoni. In addition, Mr M. A. N. Müller, Curator of the Windhoek State Herbarium, has contributed a list of presently known plant species found in the Park.

All in all, this is a compact field guide containing much useful and interesting information on the trees and shrubs of the Etosha National Park and will undoubtedly be most popular with tourists and others visiting the Park.

G. Germishuizen

Trees and Shrubs of the Cape Peninsula — A comprehensive field guide to over 230 indigenous and naturalized species by Eugene Moll & Lindsay Scott. *Rondebosch: Eco-lab Trust Fund.* 1981. Pp. x + 119, 210 × 150 mm. numerous drawings and maps, carton. Price R6,00.

This booklet obviously comes from the same stable as Eugene Moll's Trees of Natal. The cover design by Nicola Moll, when she was nine years, is the same, only in different colours. The size is again A5 but the present book is much thinner (8 against 30 mm). On the inside of the front cover is a map of the area covered, and on the inside of the back cover a second copy of the key to the main groups as well as a scale. For each species a distribution map within the area is provided, as well as one to several leaf drawings, the National tree number (where applicable), the scientific name with author and the common name according to the latest National List of Trees. Also provided are averages for leaf length and height of plant, flowering and fruiting months (for most species) and a very brief description consisting of a note on habitat and one or a few characteristics of the species. Diagnostic features shown in drawings or text are indicated with an arrow. On the last few pages there is an illustrated glossary, a brief list of titles for suggested reading and an index to both scientific and common names. The book ends with a taxonomic table of contents giving all species in the sequence and family context of Dyer's Genera. Numerous species are marked with stars or sculls-and-crossbones to indicate whether they are relatively harmless or particularly undesirable invaders. Binding and paper are of good quality and the corners are rounded, a useful anti-dog-ear measure.

The few test runs made through the keys proved to be successful but not quite smooth to begin with. The authors assume that by now their readers are familiar with the workings of an identification key. They do not warn us that unexpectedly there may be 3 or even 4 contrasts to choose between. With line spacing and lay-out not always being very critical such multiple contrasts take some getting used to. Also in both copies of the key to the major groups the page on which the most important group, group 1, begins is not given. The keys to groups end with a reference to one or two (in one instance four) pages. An average of three species is dealt with on a text page. This means that in the last identification step the reader has to chose between 3–6 (–9) species by comparing their drawings and diagnostic features. It proved easy enough to do even at the end of group 1 where the final choice may in practice involve all 16 species given on pages 38 to 42. The book makes allowances for variation in plants, and numerous species key out more than once, *Kiggelaria africana* even four times, each time with a different set of leaf drawings. The somewhat diagrammatic drawings include a piece of the branch to show the leaf attachment. For the sake of simplicity the leaf blades are shown as if they were lying in the same plane as the branches and not at 90° to them, as is the case in most trees and shrubs. In the few species, like the Australian Acacias or *Podocarpus falcatus* (here mentioned as a relatively harmless invader), where the leaf blades are naturally orientated in a vertical position, no mention is made of the fact. In their quest for extremely short descriptions the authors have often omitted very important diagnostic features which could surely have been accommodated. Examples are the red aril from which the rooikrans (*Acacia cyclops*) derives both its common and scientific names and the inflated calyx of the bladder-nut (*Diospyros whyteana*). If fruit characters were considered taboo for the work, why mention fruiting times or the winged pods of *Sesbania punicea?* No synonyms or variety names are given and the reader looking for *Olea africana* will have to run through the key which will readily guide him to *Olea europaea*. *Acacia mearnsii* is misprinted once, *Hakea suaveolens* both times. The index should have been placed last in the book, and not the taxonomic table which the reader will consult only rarely.

The work is designed as a field-guide to trees and shrubs of the Cape Peninsula. It succeeds admirably in this aim and should prove very popular. At a price of R6,00 it is excellent value for money.

O. A. Leistner

Flore des Mascareignes. (1) 31. Renonculacées à 50. Théacées. 1980. Pp. 154 and 41 plates (paperbound). (2) 64. Balsaminacées à 68. Burseracées. 1979. Pp. 58 and 12 plates (paperbound). (3) 177. Iridacées à 188. Joncacées. 1978. Pp. 113 and 20 plates (paperbound). Prices not indicated.

Four fascicles dealing with 40 families of plants on the Mascarenes have now been seen by the reviewer, and it is possible that more will be to hand by the time this review goes to press. The first fascicle was published in 1976 and reviewed in Bothalia 12,3: 578 (1978).

Each family is treated as a separate unit with its own indices to scientific and vernacular names and with the pagination and the numbering of plates beginning with 1, if there is more than one plate per family. The 203 families of ferns and flowering plants to be dealt with in this work are numbered and listed on the outer cover of each fascicle, with names of published groups printed in italics.

For each endemic genus and for the more conspicuous naturalized genera a full-page plate of line drawings, showing one to three species, is provided. The exotic family Agavaceae, represented by several species of *Agave,* is illustrated by two photos, the first to have appeared in the flora so far. The prints of these photos probably do no justice to the originals. At a rough guess, the average number of species illustrated per genus is about 2 to 3 in this work. As a result, it is very fully illustrated by comparison with most of the major Africa floras. Another respect in which this flora differs from most of the current floras of the neighbouring continent is that its literature references are largely restricted to those referring to the original publication of plant names and to works dealing specifically with the Mascarenes. Not even the Flore de Madagascar is normally referred to.

When deciding on the format the editors obviously gave special thought to horticulturalists and amateurs. The flora deals not only at length with naturalized species but also with many commonly cultivated garden plants. It also makes a special feature of vernacular names and its notes on distribution, ecology, economics and also quite often plant history, are more detailed and fuller than in most comparable works.

It is not considered necessary to give a complete list of authors of the 38 families dealt with in the present fascicles. Even at a rapid glance, it is clear that Wessel Marais, who is also one of the editors, has done the lion share of the work, with M. J. E. Coode firmly established in second place. The other nine authors have contributed no more than a single family each. It is striking that only three of the contributions were written by taxonomists outside of Kew.

Without having done any research into the matter, I would hazard a guess that the work published to date covers about 10 to 15 per cent of the total flora of the islands, and that, if the present rate of progress can be maintained, the work may be complete by the time the big clock strikes 2000. That is our birthday wish for that seemingly distant year to editors, authors and, of course, users.

O. A. Leistner

Index Herbariorum Edn 7. Regnum Vegetabile Vol. 106. Ed. E.A. Stafleu and compiled by P. K. Holmgren, W. Keuken & E. K. Schofield. *Utrecht: Bohn, Scheltema & Holkema.* 1981. Pp. 452. Price R124,60.

The new edition of Index Herbariorum, like a herbarium, contains an aggregate of information whose whole is greater than the sum of its parts. Data extracted from the entries and compared can indicate the state of herbarium taxonomy today in the world and in southern Africa. Table 1 shows the number of herbaria that fall into different size classes, and Table 2 gives more details about the ten largest herbaria in the world.

TABLE 1. — Distribution of herbaria in size classes

Size class by no. of specimens	No. of herbaria in size class
6 000 000 or above	1
5 000 000 "	3
4 000 000 "	6
3 000 000 "	4
2 000 000 "	13
1 000 000 "	22
500 000 "	39
100 000 "	240
50 000 "	168
10 000 "	505
1 000 "	515
less than 1 000	39
Total no. of herbaria	1 555

There are 49 herbaria with more than one million specimens, but only two of these are in the southern hemisphere, MEL (Melbourne, National Herbarium of Victoria) and NSW (Sydney, National Herbarium of New South Wales), both with 1 000 000 specimens. PRE (Pretoria, National Herbarium, Botanical Research Institute) is the third largest in this hemisphere, and the largest on the African continent, with 800 000 specimens. The entire Botanical Research Institute, composed of four herbaria, has well over one million specimens, as shown in Table 3. The five herbaria in the Flora of Southern Africa area that have more than 100 000 specimens are listed in Table 4. A summary of total numbers of specimens, herbaria and staff is given in Table 5.

Interesting as these figures may be in gaining a perspective of the relative size and importance of herbaria, it is nevertheless the day-to-day usefulness of the Index Herbariorum that makes it indispensible to taxonomists. The first and longest part of the book consists of the entries about each herbarium, and the second part is a number of indexes to these entries, to help find particular information about the herbaria. The herbarium entries are arranged in alphabetical order by the city, and for each herbarium is given its full name, abbreviation, address, telephone number, supporting body, year of foundation, number of specimens, area and plant group concentrated on, important collections, staff (often with details of specialization), specialization in research of the institution, associated botanic gardens, availability of loans,

TABLE 2. — The ten largest herbaria in the world, all with at least four million specimens

No. specimens	Herbarium		No. staff	No. serial publications
6 000 000 or above	P	Paris, Museum National d'Histoire Naturelle, Laboratoire de Phanerogamie	41	6
5 000 000 "	G	Geneva, Herbarium, Conservatoire et Jardin Botanique de la Ville de Geneve	15	3
	K	Kew, The Herbarium, Royal Botanic Gardens	77	5
	LE	Leningrad, Herbarium of the Department of Higher Plants, Komarov Botanical Institute	34	3
4 000 000 "	BM	London, Herbarium, British Museum (Natural History)	32	1
	MPU	Montpellier, Institut de Botanique	23	1
	NY	New York, New York Botanic Garden	30	7
	PC	Paris, Museum National d'Histoire Naturelle, Laboratoire de Cryptogamie	10	3
	S	Stockholm, Herbarium, Swedish Museum of Natural History	15	4
	US	Washington, U.S. National Herbarium, Smithsonian Institution	26	3

TABLE 3.—Size of all herbaria of the Botanical Research Institute

Herbarium	No. specimens	No. staff
PRE (Pretoria)	800 000	25
GRA (Grahamstown)	125 000	2
STE (Stellenbosch)	100 000	6
NH (Durban)	50 000	5
TOTAL	1 075 000	38

TABLE 4.—The five largest herbaria in the Flora of Southern African area, all with at least 100 000 specimens

No. specimens	Herbarium	No staff	No. serial publs
800 000	PRE Pretoria, National Herbarium Botanical Research Institute	25	5
250 000	NBG & SAM Cape Town, Compton Herbarium and South African Museum	8	1
240 000	BOL Cape Town, Bolus Herbarium University of Cape Town	4	1
125 000	GRA Herbarium, Albany Museum Botanical Research Unit	2	—
100 000	STE Stellenbosch, Government Herbarium Botanical Research Unit	6	—

TABLE 5.—Comparison of numbers of specimens, herbaria, staff and publications

	World	Flora of Southern Africa area	Botanical Research Institute
No. herbarium specimens	227 242 000	2 028 400	1 075 400
No. herbaria	1 555	36	4
No. staff	5 100	116	38
No. serial publications	693	9	5

periodical and serial works, and availability of exchange. The four indexes at the end of the volume are invaluable for finding particular information among the profusion of facts presented in the herbarium entries.

1. Index to 'important collections' — The collectors are listed alphabetically, followed by the herbaria in which their collections are housed.

2. Geographical arrangement of herbaria — by country and province or state, in alphabetical order.

3. Herbarium abbreviations — alphabetical list of abbreviations, with the city, the name and the address of the herbarium.

4. General index to personal names — the staff members listed alphabetically, with the page number of their appearance in the main section of the book.

This edition of Index Herbariorum is No. 106 in the Regnum Vegetabile series. Many of these publications have become tools of the trade of taxonomists and it is difficult to imagine working without them. One can only be grateful to botanists who have given up their time to prepare these references, so that the work of others can progress faster.

G. E. Gibbs Russell

Distribution and ecology of vascular plants in a tropical rain forest — forest vegetation in Ghana by J. B. Hall and M. D. Swaine. *The Hague, Boston, London: Junk.* 1981. Pp. xv + 383, 81 figs, 624 maps, 35 tables and 7 tabular appendices. Price Dfl. 225/US$ 112,00.

This book is by two former lecturers in the Department of Botany of the University of Ghana at Legon who, as the foreword by J. H. Francois puts it, 'Together they roamed the remotest parts of Ghana, collected, described and wrote.' The book is divided into two parts. The first part of 99 pages is titled Introduction to Ghanaian Forest and deals in eight chapters with what is forest?, variation and classification of forest, forest environment, forest flora, forest structure and physiognomy, reproduction, utilization and conservation of Ghanaian forest, and description of forest types. The second part consists of three chapters on mapping methods and map format, 624 small scale distribution maps with notes on morpholgy, taxonomy, chorology, ecology and utilization, and distribution of eleven timber species. Seven appendices then follow, giving various location and detailed data for plots, ordination scores, taxonomic data and a classification of Ghanaian timbers. There is a reference list, an index to the scientific names of plants and a general index.

This is a fascinating book for those who like to see real data which is well presented and not masked by overt over summarization. The book is nevertheless concise, lucid and well written, profusely illustrated though many of the photographs have not been well reproduced, with good figures and tables, and is otherwise technically well produced. The authors have studied the forests from many different plant ecological aspects and have used recent ecological methods and concepts, but have been practical and realistic in their approach. This is a very useful book which is also a real contribution to tropical forest ecology that future students can use.

D. Edwards

South African Parasitic Flowering Plants by Johann Visser. *Johannesburg: Juta.* 1981. Pp. 177, 218 × 302 mm, 220 figures, 68 tables, 71 maps, cloth binding. Price R45,00.

This book is aimed at both botanist and 'layman', and it should succeed in pleasing both. As is stated a number of times on the inside cover and in the author's preface, it is not intended to be a definitive work on parasitic plants, but to stimulate wider interest in the group. Though its strong accent on photography would tempt one to class it as purely a coffee-table book, a sound knowledge of botany is needed to follow the text. A good deal of extra information is also given in the form of captions to the photographs, which are consequently much more than purely decorative.

There are thirteen chapters, ten of which deal each with one of the ten families having parasitic members in South Africa. A selection of sixty-five species is illustrated. Chapter 1 deals very briefly with a number of interesting aspects of the parasitic habit. No keys are given, but it is pointed out how some of the genera differ in particular characters.

Within each of the ten chapters on families a description is given of the particular family, but in an expanded, easy-to-read style rather than in the condensed form of a purely taxonomic description. The number of genera and species, both worldwide and in South Africa, is included, as well as their distribution. Purely morphological details are interpreted in terms of pollination, survival mechanisms, host penetration, germination, etc., which makes them both relevant and interesting. About ½–1½ pages is devoted to this per chapter, the rest being taken up by photographs. One possible criticism of this part is that no mention is made of problems still to be solved or of gaps in our knowledge — one gets rather the impression that these plants are well known, and their life-histories understood.

Most of the book consists of photographs, all in colour except for the SEM pictures. All are good, and some are really beautiful; only on p.101 has the printing spoiled them. They illustrate not only habit and the whole flower, but often finer details of flower and fruit, of attachment to host, germinating seeds, underground parts, pollinators, etc. The scale is given on the RHS below each picture. The captions give much more detail than is visible in the photograph itself, and this makes up for shortness of the text *sensu stricto.*

The chapters dealing with families are followed by a chapter (4½ pp) on climate, soils and vegetation of South Africa, illustrated with maps. This is interesting, but not really relevant to the rest of the book.

Ch. 13 consists of distribution maps of the 67 species mentioned in the text, and bar graphs showing their flowering times. There is also for each a list of the known host-plants, but only genera and not species are given. There are two appendices: a short glossary, and a very short reading list which consists mostly of floras, monographs and symposium reports.

This book strikes a good balance between being enjoyable and informative. It can be recommended to both the reasonably well-informed amateur and the professional botanist, who either does not know much about parasitic plants or who confines his attention purely to their taxonomic aspects.

K. IMMELMAN

MEDICINAL PLANTS OF THE WEST INDIES by EDWARD S. AYENSU. *Algonac: Reference Publications.* 1982. pp. 282, 61 linedrawings. Price US$ 29,95.

This, the second in a series of publications entitled 'Medicinal Plants of the World', follows Dr Ayensu's 'Medicinal Plants of West Africa,' which was reviewed in Bothalia 13,4 (1981). As in the first publication, this book consists mainly of a series of descriptions of the medicinal properties attributed to the plants and some excellent illustrations, followed by a glossary of medical terms, a bibliography, species index and a medicinal index in which plants are classified according to their uses. The treatment has been greatly improved by the inclusion of an index to common names, and by the exclusion of the rather fuzzy photographs that spoilt the West African volume.

Altogether 632 species are included. They are arranged alphabetically within families which are also alphabetically arranged. For each species, the common names, area (islands within the West Indies) and uses/chemical components are recorded, together with source references. Unfortunately these references are not linked to particular information, cover literature only and do not include 'information . . . obtained from . . . many Caribbean friends,' referred to by the author in his introduction. There is, therefore, no easy way of identifying original information and its source.

The species dealt with include many naturalized exotics and pan-tropical weeds as well as indigenous species, but these are not indicated as such. This is rather frustrating in view of the author's introductory statements that 'Historical accounts indicate that the use of introduced and indigenous plants in the Caribbean was deeply rooted in slavery originating in West Africa', and that 'slaves managed to carry with them plants of economic importance'. A scan of the species covered by both the West Indian and West African books, shows 16 species in common: *Amaranthus spinosus, Spondias mombin, Commelina diffusa, Ageratum conyzoides, Bidens pilosa, Momordica charantia, Jatropha curcas, Ricinus communis, Abrus precatorius, Desmodium adscendens, Ocimum basilicum, O. gratissimum, Musa sapientum, Boerhavia diffusa, Citrus aurantifolia* and *Blighia sapinda.* An analysis of their importance and the origins of their use would have been an interesting addition — and the sort of thing that I think is needed if future volumes in this series are to be saved from being increasingly repetitive compilations.

South African readers will be interested to note that a number of local species are used medicinally in the West Indies. These include: *Dolichos lablab, Plumbago capensis, Pteridium aquilinum, Sansevieria thyrsiflora, Maytenus buxifolia, Citrullus lanatus, Cyperus rotundus, Euphorbia tirucalli, Panicum maximum* and, believe it or not, *Adansonia digitata.*

This volume is a considerable addition to the literature, an improvement on the first volume in the series, whose aim is 'to collect the widely dispersed data from different parts of the world into one convenient source-book for each region so that the scientific community and interested general public can more readily make use of such information.' I doubt, though, that it contains sufficient chemical data 'to be especially useful to phytochemists and pharmacologists.' Its usefulness could have been greatly increased by more specific referencing, and its interest increased by the inclusion of general and comparative chapters e.g. on the prevalence of the use of folk medicine, the most frequently used remedies and their possible connections with Africa and other continents.

M. J. WELLS

GUIDE FOR AUTHORS

GENERAL

Bothalia is a medium for the publication of botanical papers dealing with the flora and vegetation of Southern Africa. Papers submitted for publication in Bothalia should conform to the general style and layout of recent issues of the journal (from Vol. 11 onwards) and may be written in either English or Afrikaans.

TEXT

Manuscripts should be typed, double-spaced on one side of uniformly-sized A4 paper having at least a margin of 3 cm all round. Latin names of plants should be underlined to indicate italics. All other marking of the copy should be left to the editor. Metric units are to be used throughout. Manuscripts should be submitted in duplicate to the Editor, Bothalia, Private Bag X101, Pretoria.

ABSTRACT

A short abstract of 100–200 words in both English and Afrikaans should be provided. In the abstract the names of new species and new combinations should not be underlined.

FIGURES

Black and white drawings, including graphs, should be in jet-black Indian ink preferably on bristol board or plastic film. Lines should be bold enough to stand reduction. Lettering should be done using some printing device such as stencilling, letraset, etc. It is recommended that drawings should be twice the size of the final reduction.

Photographs submitted should be of good quality, glossy, sharp and of moderate, but not excessive contrast. Photograph mosaics should be composed by the authors themselves: the component photographs should be mounted neatly on a white card base leaving a narrow gap between each print; number the prints using some printing device.

Figures should be planned to fit, after reduction, into a width of 8 cm, 11 cm or 17 cm with a maximum vertical length of 24 cm.

The number of each figure and the author's name should be written on the back of the figure using a soft pencil.

Captions for figures should be collected together and typed on a separate paged headed *Captions for Figures.* A copy of each caption should be attached to the base of each figure.

Authors should indicate in pencil in the text where they would like their illustrations to appear.

TABLES

Tables should be set out on separate sheets and numbered in Arabic numerals.

CITATION OF SPECIMENS

In citing specimens the grid reference system should be used (Technical Note: Gen. 4.). Provinces/countries should be cited in the following order: S.W. Africa, Botswana, Transvaal, Orange Free State, Swaziland, Natal, Lesotho and the Cape. Grid references should be cited in numerical sequence. Locality records for specimens should preferably be given to within a quarter-degree square. Records from the same one-degree square are given in alphabetical order i.e. (–AC) precedes (–AD), etc. Records from the same quarter-degree square are arranged alphabetically according to the collectors' names; the quarter degree references must be repeated for each specimen cited. The following example will explain the procedure:

Natal.—2731 (Louwsburg): 16 km E. of Nongoma (–DD), *Pelser 354;* near Dwarsrand. (–CB) *Van der Merwe 4789.* 2829 (Harrismith): near Groothoek (–AB), *Smith 234;* Koffiefontein (–AB), *Taylor 720;* Cathedral Peak Forest Station (–CC), *Marriott 74.* Grid ref. unknown: Sterkstroom, *Strydom 12.*

Records from outside Southern Africa should be cited from north to south i.e. preceding those from Southern Africa. The abbreviation 'distr.' should be added to all district names e.g.:

Kenya.—Nairobi distr.: Nairobi plains beyond race course, *Napier 485.*

GIDS VIR SKRYWERS

ALGEMEEN

Bothalia is 'n medium vir die publikasie vir plantkundige artikels wat handel oor die flora van Suidelike Afrika. Artikels wat voorgelê word vir publikasie in Bothalia behoort ooreen te stem met die algemene styl en rangskikking van onlangse uitgawes van die tydskrif (vanaf vol. 11). Dit mag in Engels of in Afrikaans geskryf word.

TEKS

Manuskripte moet getik wees in dubbelspasiëring slegs op een kant van ewegroot A4-papier, met reg rondom 'n rand van minstens 3 cm breed. Latynse name van plante moet onderstreep word om aan te dui dat dit kursief gedruk moet word. Alle ander merke moet aan die redakteur oorgelaat word. Metrieke eenhede moet deurgaans gebruik word. Manuskripte moet in tweevoud ingedien word by die Redakteur, Bothalia, Privaatsak X101, Pretoria.

UITTREKSEL

'n Kort uittreksel van 100–200 woorde moet voorsien word, beide in Engels en Afrikaans. In die uittreksel moet die name van nuwe soorte en nuwe kombinasies nie onderstreep word nie.

AFBEELDINGS

Wit en swart tekeninge, insluitende grafieke, moet met pikswart Indiese ink geteken word, verkieslik op 'bristol board' of plastiekfilm. Lyne moet dik genoeg wees om verklein te kan word. Letterwerk moet gedoen word met gebruik van een of ander hulpmiddel soos letraset of 'n sjabloon. Dit is wenslik dat tekeninge tweemaal so groot as die uiteindelike verkleining sal wees.

Foto's wat ingedien word, moet van 'n hoë kwaliteit wees — glansend, skerp en van matige maar nie oordrewe kontras nie. Fotomosaïeke moet deur die skrywer self saamgestel word: die afsonderlike foto's moet netjies monteer word op 'n stuk wit karton met 'n smal strokie tussen die foto's; nommer die foto's met behulp van een of ander druk-hulpmiddel.

Afbeeldings moet so beplan word dat hulle na verkleining sal pas in 'n breedte van 8 cm, 11 cm of 17 cm met 'n maksimum vertikale lengte van 24 cm.

Die nommer van elke afbeelding sowel as die skrywer se naam moet op die rugkant van die afbeelding geskryf word met 'n sagte potlood.

Onderskrifte vir afbeeldings moet bymekaar getik word op 'n afsonderlike bladsy met die opskrif *Onderskrifte vir Afbeeldings.* 'n Afskrif van elke onderskrif moet aan die onderkant van elke afbeelding vasgeheg word.

Skrywers moet met potlood in die teks aandui waar hulle graag hulle afbeeldings wil hê.

TABELLE

Tabelle moet op afsonderlike velle papier kom en genommer word met Arabiese nommers.

SITERING VAN EKSEMPLARE

Wanneer eksemplare siteer word, moet die ruitverwysing stelsel gebruik word (Tegniese Nota: Gen. 4). Provinsies/lande moet in die volgende volgorde siteer word: Suidwes-Afrika, Botswana, Transvaal, Oranje-Vrystaat, Swaziland, Natal, Lesotho en die Kaapprovinsie. Ruitverwysings moet in numeriese volgorde siteer word. Lokaliteitsrekords vir eksemplare moet verkieslik tot binne kwartgraadvierkante gegee word. Rekords uit dieselfde eengraadvierkant word in alfabetiese volgorde aangebied, nl. (–AC) kom voor (–AD) ens. Rekords uit dieselfde kwartgraadvierkant word alfabeties gerangskik volgens die versamelaars se name, en die kwartgraadverwysings moet herhaal word vir elke eksemplaar wat siteer word. Die volgende voorbeeld sal die metode verduidelik:

Natal.—2731 (Louwsburg): 16 km O. van Nongoma (–DD), *Pelser 354;* naby Dwarsland (–CB), *Van der Merwe 4789.* 2829 (Harrismith): naby Groothoek (–AB), *Smith 234,* Koffiefontein (–AB), *Taylor 720;* Cathedral Peak Bosboustasie (–CC), *Marriott 74.* Ruitverwysing onbekend: Sterkstroom. *Strydom 12.*

Rekords van buite Suidelike Afrika moet siteer word van noord na suid, d.w.s. dit gaan dié van Suidelike Afrika vooraf. Die afkorting 'distr.' behoort by alle distriksname gevoeg te word, bv:

Kenya.—Nairobi-distr.: Nairobivlakte anderkant die renbaan, *Napier 485.*

REFERENCES

References in the text should be cited as follows: 'Jones (1955) stated . . .' or '. . . (Smith, 1956)' when giving a reference simply as authority for a statement. The list of references at the end of the article should be arranged alphabetically and the literature abbreviation used should conform to the World List of Scientific Periodicals (1965) or the list of Literature Abbreviations (Technical Note: Tax. 6 AN 1) issued by the Botanical Research Institute, thus:

Brown, N. E., 1909. Asclepiadaceae. In W. T. Thiselton-Dyer, *Fl. Cap.* 6,2: 518–1036. London: Lovell Reeve.

Hutchinson, J., 1946. *A botanist in Southern Africa.* London: Gawthorn.

Kruger, F. J., 1974. *The physiography and plant communities of the Jakkalsrivier Catchment.* M.Sc. (Forestry) thesis, University of Stellenbosch (unpublished).

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If, as in many taxonomic papers, periodicals or books are mentioned in the text, usually in the species synopsis, they should be cited as in the following examples: Gilg & Ben. in Bot. Jb. 53: 240 (1915) and Burtt Davy, Fl. Transv. 1: 122 (1926).

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Brown, M. E. Asclepiadaceae. In W. T. Thiselton-Dyer, *Fl. Cap.* 6,2: 518–1036. London: Lovell Reeve.

Hutchinson, J. 1946. *A botanist in Southern Africa.* London: Gawthorn.

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Morris, J. W., 1969. An ordination of the vegetation of Ntshongweni, Natal. *Bothalia* 10: 89–120.

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EDITORIAL

As Editor of Bothalia and Chairman of the AETFAT Editorial Committee, I would like to express my appreciation to members of the Committee, who refereed the 123 papers read at the AETFAT Congress. 115 of these papers are included in these Proceedings. The members of the Committee were: Professors J. G. Small and G. K. Theron, Drs J. M. Anderson, D. Edwards, R. P. Ellis, F. Getliffe Norris, G. E. Gibbs Russell, O. A. Leistner, J. W. Morris and J. V. van Greuning, and Messrs P. Bamps (who specially checked the French papers), E. G. H. Oliver and C. H. Stirton. Theirs was an enormous task and they did a good job.

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D. J. B. KILLICK

Pretoria
1 September 1982

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The migration and evolution of floras in the southern hemisphere

P. H. RAVEN*

ABSTRACT

As modern groups of angiosperms have appeared over a period of more than 80 million years, the relative position of the southern continents has changed. For the first 20 m.y. of this period, opportunities for migration were good between Africa and Europe, and this constituted the main pathway for migration between the northern and southern hemispheres. South America progressively moved away from Africa and towards North America over the past 90 m.y. Southern South America and Australasia shared a rich, warm temperate rainforest flora until about 40 m.y. ago. The development of modern climates during the past 10 m.y. has set up modern patterns of vegetation.

RÉSUMÉ

LA MIGRATION ET L'ÉVOLUTION DES FLORES DE L'HÉMISPHERE AUSTRAL

Alors que les groupes modernes d'angiospermes sont apparus au cours d'une période de plus de 80 millions d'années, la position relative des continents du Sud a changé. Durant les premiers 20 millions d'années de cette période, les occasions de migration entre l'Afrique et l'Europe furent favorables et ceci constitua la voie principale de la migration entre les hémisphères sud et nord. L'Amérique du Sud s'écarta progressivement de l'Afrique en direction de l'Amérique du Nord au cours des 90 derniers millions d'années. L'Amérique du Sud et l'Australasie partagèrènt une flore forestière riche et tempérée chaude jusqu'à il y a 40 millions d'années. Le développement des climats modernes pendant les derniers 10 millions d'années a mis en place des types de végétation modernes.

The patterns of migration and evolution of floras in the southern hemisphere have occupied the attention of botanists and geographers for well over a century, ever since the principal patterns became evident following the intensive exploration of the far-flung southern lands during the mid-19th century and subsequently. It will be the purpose of this brief review to set the stage for the papers that follow by providing an overview of (1) the past positions and movements of the relevant continents and islands; (2) the history of the angiosperms; and (3) the evolution of vegetation types in the southern lands. We shall concern ourselves with the last 135 m.y. of earth history, the period during which the angiosperms appeared in the fossil record and later assumed worldwide dominance. The first six papers listed in the references are basic to this entire paper and will not be repeated.

West Gondwanaland, consisting of Africa and South America, began to split apart in the South Atlantic about 125–130 m.y. BP with the last direct land connection being severed about 90 m.y. BP. Even subsequently, 88–86 m.y. BP, the Rio Grande-Walvis ridges would have formed an almost continuous overland series of stepping stones across the South Atlantic at about 30°S lat, with the Brazil-Angola Basin isolated to the north and the Cape-Argentine Basin to the south (Kennedy & Cooper, 1975, Van der Linden, 1980 and Reyment, 1980). Bonati & Chermak (1981), basing their conclusions on recent deep sea drilling results, discuss the probable role of shallow or emergent crust in the South Atlantic even into the early Cenozoic (less than 65 m.y. ago), which they believe may have formed chains of islands or intermittent land bridges over which migration of plants and animals could have taken place. Thus dispersal was more direct between Africa and South America than between North and South America until about 45 m.y. BP. South America gradually converged on North America during the past 90 m.y., with the ultimate elevation of the Isthmus of Panama 3,1–3,6 m.y. BP connecting them by land for the first time (Marshall *et al.*, 1979).

At the start of the Cretaceous, 135 m.y. BP, East Gondwanaland consisted of India, Australia and its bordering lands, and Antarctica, with direct overland migration possible to West Gondwanaland *via* both Antarctica and India-Madagascar. From about 135 to about 80 m.y. BP, India separated slowly from this landmass, providing a fairly direct but interrupted dispersal route across the Indian Ocean between Africa and Australia throughout this period. Starting about 80 m.y. BP, India commenced rapid northward movement until its collision with Asia about 53 m.y. BP; its subsequent movement northward has thrust up the Himalayas and the Tibetan Plateau.

Antarctica has been in its present polar position for at least 90–100 m.y., possibly with some rotational movement. The Tasman Sea between New Caledonia-New Zealand and Australia-Antarctica formed in the period 82–60 m.y. BP, with a considerable amount of land elevated between New Caledonia and Queensland, as well as between New Caledonia and New Zealand, until the end of this period. Australia began to separate from Antarctica and move northward about 53 m.y. BP, with more or less direct migration through the Tasmanian area *via* the South Tasman Rise between Australia and Antarctica possible until about 38 m.y. BP. There is no evidence that any part of Southeast Asia or Indonesia was a part of Gondwanaland and moved northward at any time since the start of the Cretaceous (Hamilton, 1979). As Australia commenced its northward movement, all of New Guinea and much of northern Australia were subsea, so that the northernmost land on the Australian plate was at about 38°S lat, approximately the present latitude of Melbourne.

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New Guinea began to appear above the sea for the first time about 40 m.y. BP, and at that time was at about 15°S lat, near the present latitude of Cairns. It moved steadily northward with the Australian plate, coming into contact with the proto-Indonesian island arc and coalescing into an extensive land area about 15–20 m.y. BP (Axelrod & Raven, 1982). Therefore, at the start of the northward movement of the Australian plate, its northernmost land was separated from the island arc at the south edge of tropical Asia by about 3 000 km of largely open water. For comparison, the present gap between Africa and South America is about 2 500 km. By 15 m.y. BP, New Guinea constituted an extensive land area immediately adjacent to lands occupied by the rich and diverse biota of Southeast Asia, a relationship that readily accounts for the predominantly Asian nature of its plants and animals.

For the past 40 m.y. or so, South America has been converging on North America, with ever-increasing opportunities for dispersal between them. Connections between Antarctica and southern South America *via* West Antarctica, an archipelago of closely spaced islands, seem to have been quite direct until about 28 m.y. BP (Tarling, 1980), but the last opportunity for more or less direct migration overland between South America and Australia *via* Antarctica was lost at least 10 m.y. earlier, as reviewed above.

From the start of the period being considered here, 135 m.y. BP, until about 50 m.y. BP, a gap of about 3 000 km, as mentioned above, separated the nearest land areas in Australasia from those in Asia. During the same period of time, a gap that was initially as large between South America and North America closed to about half that distance. Meanwhile, Africa, during the interval 148–80 m.y. BP, converged some 2 800 km toward Europe, with continuing compression until about 63 m.y. BP, resulting in the formation of the Alpine system. For about the next 10 m.y., Africa moved away from Europe. These relationships indicate unequivocally that during the first half of angiosperm history, the only relatively direct connections between the northern and southern hemispheres were those involving Europe and Africa. From about 53 m.y. BP until about 18 m.y. BP, when connections were re-established, Africa again converged on Europe, with increasingly great opportunities for dispersal of plants and animals between them.

Before discussing the relevance of these continental movements for the distribution of angiosperms, it is first necessary to review the history of the group in broad outline. The following comments will depend heavily upon the outstandingly useful review by Muller (1981) of fossil pollen records of extant angiosperms, as well as on the references mentioned above. Angiosperms first appear in the fossil record of southern Eurasia and North America and that of northern Africa and South America about 120 m.y. BP, with the sort of tricolpate pollen that is characteristic of most dicotyledonous plants appearing throughout the same area about 10–15 m.y. later. By about 80 m.y. BP, a number of extant groups had appeared, including Chloranthaceae, Ulmaceae, Fagaceae (*Nothofagus*), Betulaceae, Myricaceae, Lecythidaceae, Haloragaceae, Sapindaceae-Cupanieae, and Aquifoliaceae. Additional groups appear progressively, with a majority of modern families seemingly present by about 45 m.y. BP and nearly all presumably so by the start of the Miocene (22,5 m.y. BP). Looking at these relationships another way, angiosperms became dominant in fossil floras over ferns and gymnosperms about 90 m.y. BP in the areas where they first appeared, although the great majority of the angiosperms in existence in those ancient times had pollen that cannot be related directly to that of existing taxa.

Both northward and southward from southern Eurasia and North America, northern South America and Africa, the angiosperms as a whole, as well as particular groups of angiosperms, appear more recently. This relationship strongly supports a hypothesis of origin in the area outlined, followed by progressive poleward migration. In Australasia, for example, the earliest recognizable angiosperm pollen appears about 107 m.y. BP (Raven, 1982), followed by the appearance of extant taxa about 80 m.y. BP and by the ascendancy to dominance in fossil floras of the group at about 70 m.y. BP, at least 20 m.y. after this had occurred in more tropical regions. Similar age relationships appear to have been true for southern South America also, which seems to have had fossil floras more similar to those of Australia, Antarctica, and India than to those of northern South America until about 50 m.y. BP.

In the light of these relationships, we divide the history of extant groups of angiosperms roughly into three phases: (1) 80–60 m.y. BP, first modern families present; (2) 60–20 m.y. BP, most modern families present; (3) 20 m.y. to present, essentially modern floras. Each period will now be discussed in terms of its geographical relationships and the most feasible pathways for migration and dispersal at that time.

During the first period, migration between the northern and southern hemispheres would have been almost exclusively between Europe and Africa. All of the southern lands were in relatively direct contact when the first existing families of angiosperms began to appear in the fossil record, with Africa and South America relatively close and water gaps across the Indian Ocean made much narrower than at the present position of India.

The following 40 m.y. commenced with relatively poor contacts between the northern and southern hemispheres. The floras of Africa, South America, and Australasia evolved mostly in isolation during this period. By the end of the period, overland connections between Africa and Europe had been established, North and South America were close enough that there seems to have been an active exchange of plants and invertebrates, and plants and animals of Asian origin were entering New Guinea in large numbers from the north and west. New Caledonia became separated from Australia as a 'living museum' of the plants and animals that populated that continent at the start of this period. A common, rich, warm temperate flora and fauna found in southern South America and Australia at the start of the period was fragmented as the world climate began to deteriorate.

During the past 20 m.y., the cooling trend in the southern hemisphere that apparently began with the formation of a water passage around Antarctica 10–15 m.y. earlier was accelerated (Raven, 1982). The East Antarctic ice sheet began to spread rapidly about 16 m.y. BP and reached its greatest extent about 13 m.y. BP as the southern hemisphere ice age began. The maximum extension of ice in the south caused a worldwide lowering of sea level that precipitated the Messinian Crisis in the Mediterranean as it was cut off from the Atlantic (Schnitker, 1980). The West Antarctic ice sheet formed over an archipelago starting about 9 m.y. BP, pushing the world climate into its contemporary dimensions with extremely dry conditions during the past 5–6 m.y. The earliest glacial deposits in South America are 7,2–5,4 m.y. old. Widespread ice sheet formation in the northern hemisphere, almost certainly triggered by events in the south, began 3–2,5 m.y. ago.

The implications of the continental movements and climatic changes just reviewed for the migration of organisms are evident. During the past 20 m.y., when the continents may be thought of as occupying their present positions, climatic change and the evolution of extreme, drought-adapted vegetation types has gradually led to increased diversification at the generic and specific levels, with progressively decreased opportunities for migration by taxa occupying humid forest and corresponding increased opportunities for migration by those of arid-land and mountain communities. For example, the migration of the plants and animals of aseasonal forest around the Indian Ocean between Africa and tropical Asia was essentially uninterrupted 20 m.y. ago, but now involves huge gaps. By the same token, Africa, South America, and Australia were largely clothed with evergreen rainforest of tropical to warm temperate character 20 m.y. ago, and the development of the characteristic vegetation types seen today has occurred subsequently.

In both South America and Africa, thousands of metres of uplift during this period has expanded habitats for the plants and animals characteristic of cooler areas to the north and to the south, and greatly enhanced the opportunities for north-south migration. The spreading aridity associated with the cool currents resulting from massive glaciation, particularly during the past several million years, has decimated the flora of Africa and allowed savannas to spread on a continental scale at the expense of the rainforest. In South America, the aridity associated with cool water offshore has largely been confined to the areas west of the Andes, with extensive areas of humid forest persisting to the east, except at times of maximum glaciation. The uplift of the Andes, with their fantastic array of habitats lying across the full tropics, as well as the persistence of rainforest across much of the Amazon basin, seem to be the leading factors involved in the great difference between the numbers of angiosperm species of tropical South America (more than 80 000) as compared with tropical Africa (roughly 30 000 *fide* Brenan, 1978), despite the much greater size of the latter. The flora of Madagascar, proportionately much richer than that of continental Africa (Leroy, 1978), deserves continued special attention, especially in view of its threatened status (Rauh, 1979).

In Australia, a rich subtropical to warm temperate rainforest that occupied most of the continent until perhaps 12 m.y. ago is now restricted to a series of rainforest patches scattered from Queensland to Tasmania originally amounting to no more than 20 000 km^2, and now slashed back to only half that extent. Australia is now three-quarters desert, with the remainder largely savanna and sclerophyll communities rich in endemics. In these tiny patches of rainforest that survive in Australia, together with the additional 300 km^2 of rainforest in New Caledonia (1350 of 1499 species, 82 of 365 genera, and 5 of 108 families endemic *fide* Morat, Veillon & Mackee, 1981), and the more extensive areas in New Guinea and New Zealand occurs the most remarkable array of archaic angiosperms found anywhere in the world, these probably having survived in the outlying extremities of angiosperm migration, where they have not been replaced by migration from the central areas of radiation in northern Africa, northern South America, and adjacent lands of the northern hemisphere. Although southern South America demonstrably shared this flora in the early Tertiary, it has largely become extinct there, presumably as a result of mountain-building and glaciation.

Axelrod (1979) has provided a very full account of the spread of deserts to a continental scale during the past few million years; they are more extensive at present than has ever been the case in the past. The kinds of sclerophyllous plant communities that occur chiefly in areas of the world with a mediterranean (summer-dry) climate, and in which families such as Proteaceae and Myrtaceae have proliferated to such a remarkable degree, seem to owe their origins to the preadaptation of such plants to these recently derived climates. Especially in Australia and southern Africa, such plants probably originated starting approximately 60 million years ago on areas of highly infertile soil (Johnson & Briggs, 1981). Why the fynbos in southern Africa has spread so extensively under the influence of man, while comparable plant communities in Australia appear to have contracted, is unknown.

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Africa and Precambrian biological evolution

A. H. KNOLL*

ABSTRACT

African sedimentary rocks and their contained fossils have played a fundamental role in the unravelling of Precambrian biological history. Various lines of evidence including stromatolites, filamentous and coccoidal microfossils, stable isotope ratios, organic carbon distribution, and oxide facies iron formation suggest that a complex prokaryotic ecosystem fueled by photosynthesis, and perhaps including aerobic photoautotrophs, existed as early as 3 500 m.y. ago. The primary sources of data on early Archean life are rock sequences in southern Africa and Australia. The diversity of later Archean (ca. 2 700 m.y.) communities is attested to by abundant and varied stromatolites found in Zimbabwe.

The extensive growth and consolidation of continents that heralded the Proterozoic Eon had profound effects on the earth's biota. Primary productivity must have increased substantially, resulting in the establishment of an 0_2-rich atmosphere, and, subsequently, the radiation of aerobic respirers. Southern African sequences provide critical evidence bearing on this crust/atmosphere/biota interaction; however, the best known microfossils of this age come from North America.

Upper Proterozoic sedimentary rocks abound in Africa. Stromatolites from northwestern Africa have been well studied; however, microfossil occurrences remain but sketchily described. Contemporaneous sequences from Scandinavia and Australia document the initial radiation of eukaryotes in the planktonic realm, as well as a terminal Precambrian episode of extinction among plankters. Early heterotrophic protists are known from several continents. The Nama Group of South West Africa/Namibia contains important evidence of early invertebrates.

In general, Precambrian evolution can be viewed as a series of increasingly elevated biological plateaus connected by steps marking relatively short periods of evolutionary innovation and radiation. With each step, communities have increased in complexity, but prokaryote mediated element cycles established early in biological history remain at the core of functioning ecosystems.

RÉSUMÉ

L'AFRIQUE ET L'ÉVOLUTION BIOLOGIQUE PRÉ-CAMBRIENNE

Les roches sédimentaires africaines et leur teneur en fossiles ont joué un rôle fondamental dans l'élucidation de l'histoire biologique pré-cambrienne. Diverses preuves incluant des stromatolites, des micro-fossiles filamenteux et coccoidaux, des proportions stables d'isotopes, la distribution du carbone organique et la formation d'oxyde de fer suggèrent qu'un écosystème prokaryotique complexe, alimenté par photosynthèse et incluant peut-être des photoautotrophes aérobiques existaient déja il y a 3 500 millions d'années. Les premières sources de données sur le début de la vie archéenne sont les séries de roches de l'Afrique australe et de l'Australie. La diversité des communautés durant la suite de l'Archéen (ca. 2 700 millions d'années) est attestée par les stromatolites abondants et variés trouvés au Zimbabwe.

La croissance importante et la consolidation des continents qui annoncèrent l'âge protérozoîque eurent de profondes influences sur la faune et la flore terrestres. La productivité primaire doit s'être accrue substantiellement, aboutissant à l'établissement d'une atmosphère riche en 0_2 et, par la suite, l'expansion de respirateurs aérobiques. Les séries de l'Afrique du Sud fournissent la preuve de l'interaction: croûte/atmosphère/flore et faune; cependant les micro-fossiles les mieux connus de cet âge proviennent de l'Amérique du Nord.

Les roches sédimentaires du Protérozoîque supérieur abondent en Afrique. Les stromatolites de l'Afrique du Nord-Ouest ont été bien étudiés; cependant la présence de micro-fossiles reste à peine esquissée. Des séries contemporaines de Scandinavie et d'Australie nous renseignent sur l'apparition d'eukaryotes dans le domaine planctonique, aussi bien que sur un épisode d'extinction de certains constituants du plancton, à la fin du Précambrien. Les protistes hétérotrophiques primitifs sont connus dans plusieurs continents. Le groupe Nama du Sud-Ouest africain/Namibie, comporte une preuve importante des premiers invertébrés.

En général l'évolution pré-cambrienne peut être vue comme une série de plateaux biologiques de plus en plus élevés, connectés par des échelons marquant des périodes relativement courtes d'innovation et de radiation évolutionnaires. A chaque échelon, les communautés augmentèrent en complexité, mais les cycles d'éléments interposés prokaryotes établis à l'origine de l'histoire biologique demeurent au coeur des écosystèmes en opération.

INTRODUCTION

The extensive Precambrian terrains of Africa have played an important role in the study of early crustal, atmospheric, and biological history. The purpose of this paper is to review briefly the evidence for Precambrian biological evolution, making a clear distinction between facts and the interpretations, however reasonable, that have been drawn from those facts. Major emphasis will be placed on African rocks, the evidence of early life they contain, and the potential for further paleontological investigation on this continent (Fig. 1).

THE ARCHEAN

Precambrian time, which extends from the origin of the earth some 4 600 m.y. ago to the first appearance of diverse well-skeletonized invertebrates 590 m.y. ago, is divisible into two major periods, the Archean and Proterozoic Eons. The boundary between the eons at approximately 2 500 m.y. B.P. is not arbitrarily drawn; it reflects the separation of

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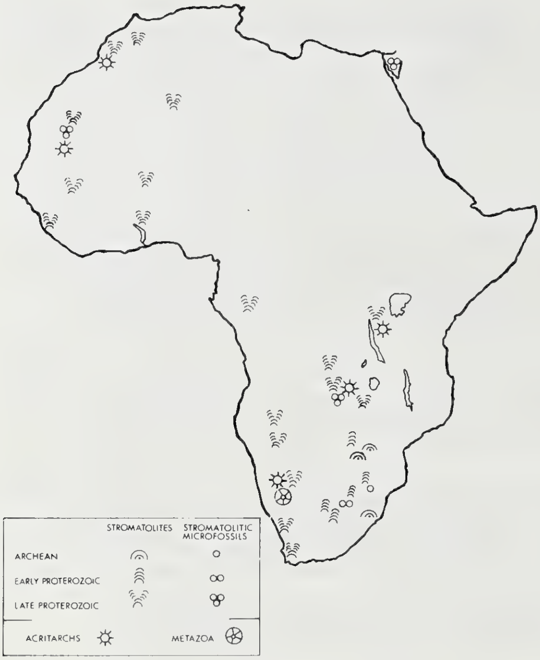

FIG. 1. — Distribution of known Precambrian fossils and stromatolites in Africa.

two periods of earth history characterized by markedly contrasting tectonic and, hence, sedimentary styles. The Proterozoic earth featured large stable continents and linear geosynclines similar in dimensions and sedimentary-tectonic evolution to those of more recent periods. In the Archean, on the other hand, cratonic areas were limited; the preponderance of ultramafic to intermediate (and sometimes felsic) lavas and poorly sorted greywacke sandstones and shales in Archean supracrustal sequences attests to the fact that different tectonic patterns shaped the early earth's surface. Perhaps the easiest way to envision the Archean earth is to imagine that the entire globe resembled the present day Indonesian archipelago. The Archean-Proterozoic boundary thus represents a period of large scale cratonization, a fundamental geological shift that I believe must have had profound consequences for the evolving biota.

If we strip our knowledge of early Archean (>3 000 m.y.) biology of all interpretation and limit ourselves to the facts, we can say the following: 3 500 m.y. ago there existed organisms, some of which were filamentous. As is well-known to African scientists, the extraordinary antiquity of life was first established on the basis of the micropaleontological study of carbonaceous cherts from the Onverwacht and Fig Tree Groups of the Barberton Mountain Land, South Africa and Swaziland (Pflug, 1966; Barghoorn & Schopf, 1966; Schopf & Barghoorn, 1967). Many authors have illustrated Onverwacht and Fig Tree microstructures interpreted as fossil micro-organisms; however, many or most of these structures are abiogenic (Schopf, 1976, 1980b). The microstructures that most likely do represent the preserved organic remains of prokaryotic organisms are micron sized bacterial rods reported by Barghoorn & Schopf (1966) and 2–4 μm spheroids, some in various stages of division, discussed by Muir & Grant (1976) and Knoll & Barghoorn (1977). Fig. 2.6–2.9.

The best direct evidence of early life comes from the improbably named North Pole Barite of Western Australia in which a variety of silicified microstructures, including unmistakable filamentous microfossils, have been discovered (Awramik *et al.*, 1983). Unfortunately, prokaryotes have simple morphologies and diverse physiologies; therefore, it is impossible to draw metabolic conclusions from any of these remains. Also occurring in the North Pole rocks are stromatolites (Walter *et al.*, 1980; Lowe, 1980) — laminated organo-sedimentary structures built by the trapping and binding and precipitating activity of micro-organism populations. Today, stromatolites accreting in coastal environments that resemble the North Pole depositional setting are built by cyanobacteria. In hot springs, such as those found in Yellowstone Park, the photosynthetic bacterium *Chloroflexus* also build mats, in association with the coccoid blue-green *Synechococcus* (Brock, 1978). It is tempting to conclude that the North Pole stromatolites were built by aerobic photoautotrophs, but this is by no means certain (Walter *et al.*, 1980). The sequence containing the Australian fossils has been dated by zircons at 3 452 ± 12 m.y. (Pidgeon, 1978) and at 3 520 ± 60 m.y. using Sm-Nd (Walter *et al.*, 1980).

Those meagre data constitute the unadorned, but unimpeachable facts about life's earliest known record; however, by even conservative interpretations of several collateral lines of evidence, a fuller picture of early ecosystems emerges. Stable carbon isotope ratios in Archean organic matter and co-occurring carbonates suggest that 3 500 m.y. ago, as now, photosynthesis lay at the heart of the terrestrial carbon cycle (Eichmann & Schidlowski, 1975; Schidlowski, 1978). Whether this photosynthesis was aerobic or anaerobic cannot be unequivocally determined.

Dissimilatory sulfate reduction also leaves an isotopic record in sedimentary rocks, and intriguingly, pyrites from the Fig Tree Group and other sequences older than 2 800–3 100 m.y. do not bear the earmarks of biological activity (Schidlowski, 1979; Monster *et al.*, 1979). The suggestion that follows from this is that sulfate-reducing bacteria may have arisen relatively late in the Archean. Another indirect line of evidence is the sizeable deposits of oxidized sedimentary iron formation found in the Barberton Mountain Land, as well as in other Archean sequences as old as 3 800 m.y. (the Isua supracrustals; see Appel, 1980). Such deposits cannot form in the absence of a source of free oxygen, and whereas some workers have suggested that photolytic breakdown of water vapor in the upper atmosphere could have supplied the necessary oxygen, others maintain that only aerobic photosynthesis could produce 0_2 at the rates necessary to oxidize the iron preserved in Archean sedimentary rocks (Walker, 1978).

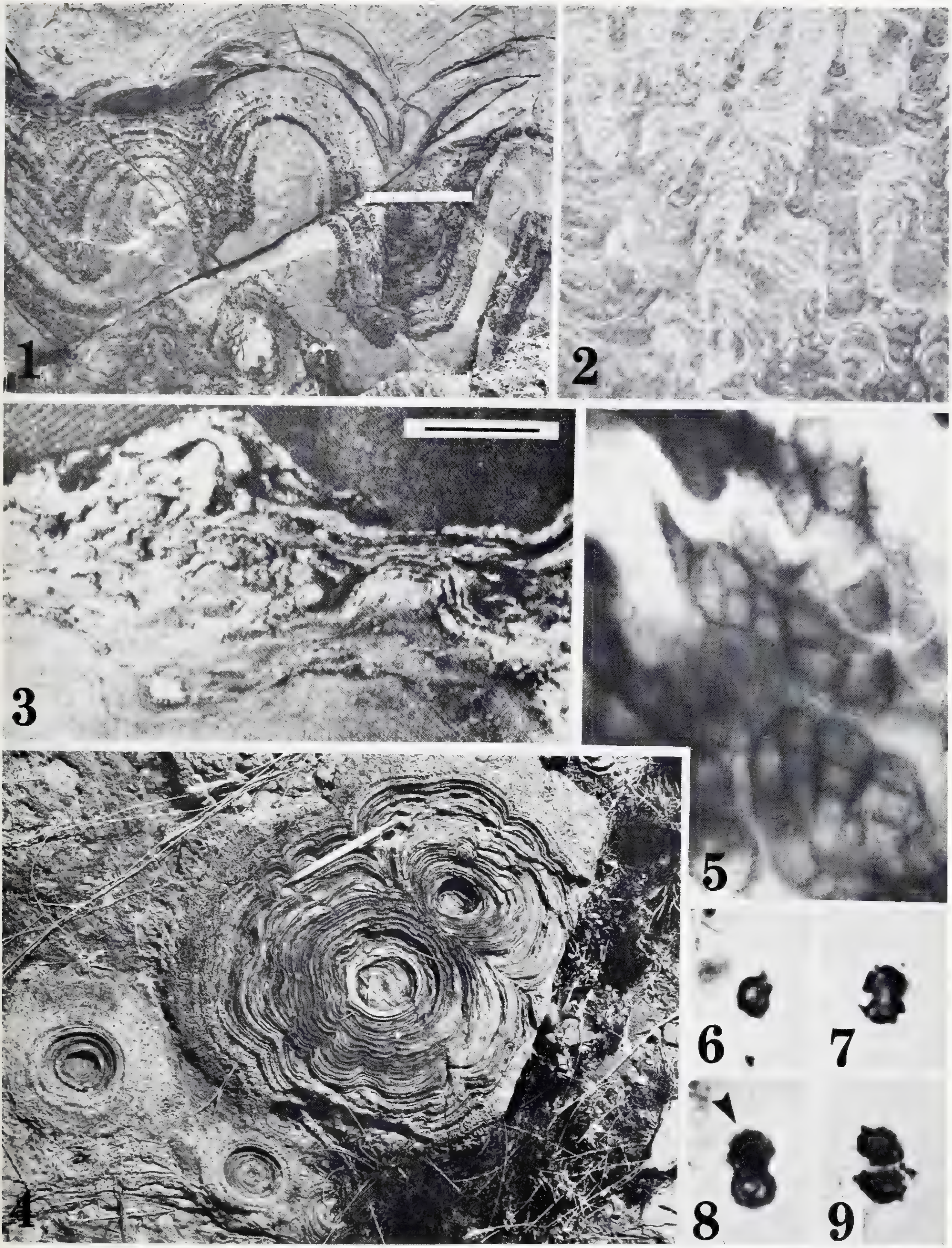

FIG. 2. — Precambrian stromatolites and microfossils. Bar in Fig. 2.3 = 2,5 cm in 1 (note 2 cm bar scale), 30 mm in 2, 7,5 mm in 3, 40 μm in 5, and = 10 μm in 6–9.

1 & 2, stromatolites from the Archean (2 700 m.y. B.P.) Belingwe Greenstone Belt, Zimbabwe; 3, cross-section through a microbially laminated (stromatolitic) carbonate from the Archean (3 000 m.y. B.P.) Pongola Supergroup, South Africa; 4, surface outcrop view of domal stromatolites from the Early Proterozoic Transvaal Supergroup, South Africa; 5, *Paleopleurocapsa wopfnerii* Knoll, Barghoorn & Golubic, a pleurocapsalean cyanobacterium from the Late Precambrian Skillogalee Formation, Australia; 6–9, Archean (3 400 m.y. B.P.) coccoidal microfossils showing various stages in cell division, from the Fig Tree Group, South Africa. 1 & 2, from Martin *et al.*, 1980, courtesy of the authors and reproduced by permission of Elsevier Publishing Company; 3, courtesy of T. R. Mason and reproduced by permission of Macmillan Journals, Ltd.; 4, courtesy of K. A. Eriksson and reproduced by permission of Elsevier.

One can hypothesize abiological ways of fractionating carbon isotopes, producing low atmospheric concentrations of oxygen, or even forming the prodigious amounts of organic matter preserved in early Archean sedimentary rocks (Reimer *et al.*, 1979); however, the most parsimonious solution to the problem of interpreting this array of data is to suggest that in the oldest unmetamorphosed supracrustal sequences on earth, we can see the record of a metabolically diverse prokaryotic ecosystem that almost certainly included photoautotrophs and which may have included cyanobacterial photosynthesizers.

In younger Archean sequences, one finds evidence of greater microbial diversity and, perhaps, sophistication. Micro-organisms preserved in cherts of the 2 800 m.y. old Fortescue Group, Australia (Schopf, 1980), include filaments that are morphologically indistinguishable from modern oscillatorian cyanobacteria. Of even greater interest are the morphologically diverse stromatolites found in limestones of the 2 700 m.y. old Belingwe Greenstone Belt in Zimbabwe (Martin *et al.*, 1980, Fig. 2.1 & 2.2) and the somewhat older microbially laminated carbonates from the Pongola Supergroup, South Africa (Mason & von Brunn, 1977, Fig. 2.3). Our available sample of Archean life is so small that it would be perilous to interpret the microfossil and stromatolite evidence as indicating a true evolutionary diversification of microbes between 3 500 and 2 700 m.y. B.P. (although that is certainly one plausible explanation for the record as read literally); an alternative that I will present, but not defend, is that in the early Archean, prokaryotes diversified rapidly and within a few hundred million years developed most of the physiological pathways possible in an oxygen poor environment. Such a hypothesis is consistent with the prokaryote phylogenetic patterns generated by Fox *et al.* (1980) on the basis of 16S ribosomal RNA characterization, as is the logical corollary that aerobic microbial physiologies radiated quickly following the subsequent accumulation of significant atmospheric 0_2 concentrations.

Increased understanding of Archean evolution will require extensive paleontological investigation of sedimentologically well characterized ancient sequences. Relatively unmetamorphosed rock packages in Botswana, Zimbabwe, South Africa, and Swaziland (including further exploration of the Barberton Mountain Land) are likely to yield much useful information. This paleontological research must be coupled to innovative geochemical work, increasingly sophisticated nucleic acid sequencing of extant prokaryotes, and improved models of the Archean crust, ocean, and atmosphere that provided the context for early evolution.

THE EARLY PROTEROZOIC

Latest Archean alluvial and lacustrine sedimentary rocks from the Witwatersrand Basin, South Africa, contain critical evidence bearing on atmospheric and, hence, biological evolution. Along with the gold for which these beds are justly famous, Witwatersrand conglomerates contain placers of detrital uraninite ($U0_2$). Uraninite is quickly oxidized in the presence of oxygen, so the fact that these Witwatersrand grains were weathered and eroded from an igneous source rock, transported by streams for some unknown distance, and then deposited in river bars and lacustrine delta distributory fans without ever being oxidized suggests that atmospheric oxygen levels were not in excess of 1% Present Day Atmosphere Level (PAL) (Grandstaff, 1980). It is possible to form isolated accumulations of uraninite beneath a oxygen-rich atmosphere by somehow coating grains to shield them from oxidation; uraninite can be found in modern stream gravels of the Indus River (Simpson & Bowes, 1978); however, the Witwatersrand conglomerate is not a unique deposit.

Earliest Proterozoic alluvial sediments from North America, Europe, Australia, and South America also contain detrital uraninite (Robertson *et al.*, 1978), and in each case, the immediately superjacent beds include red beds — sand-stones and shales tinted by tiny grains of iron oxide – but no uraninites. In fact, there are no significant accumulations of detrital uraninite in any sequences younger than 2 300–2 200 m.y. Conversely, red beds, which are unknown in older deposits, are common after this time. The conclusion drawn from this is that the atmosphere first became oxygen rich in the Early Proterozoic Era (Cloud, 1968, 1972, 1974; Frarey & Roscoe, 1973; but see Dimroth & Kimberley, 1976, for a dissenting view).

Why should the crustal transition from Archean to Proterozoic be accompanied by an equally epochal atmospheric change? Again, African rocks, specifically the Transvaal Supergroup of South Africa and the in part correlative Lomagundi Group, Zimbabwe, provide important clues for interpretation. Transvaal and Lomagundi dolomites constitute the earliest evidence of laterally extensive shallow marine carbonate platform deposits. A wide variety of stromatolites have been described from Transvaal dolomites (Truswell & Eriksson, 1975; Bertrand-Sarfati & Eriksson, 1977, Fig. 2.4).

The paleontological fact of high stromatolite diversity can be extrapolated reasonably to the interpretation of high microbial community diversity, with cyanobacteria almost assuredly being the dominant mat builders and primary producers. The extensive area covered by Transvaal and Lomagundi carbonates indicates that for the first time in earth history, broad, stable, shallow marine platforms were available for colonization by photoautotrophs. That is to say, the geological evolution of large cratons at the end of the Archean must have had biological consequences in terms of microbial ecology and productivity (Knoll, 1979). I am not arguing that the earth went from no cratons to full scale continents in a geological instant marking the Archean/Proterozoic boundary, but rather that continental growth very likely followed a logistic curve with the greatest rate of growth occurring at the end of the Archean. The biological consequences of this would be a greatly increased area available for cyanobacterial colonization, a significant increase in benthic productivity per unit area due to the more hospitable nature of most photic zone environments, and an increased level of whole ocean primary productivity associated with nutrient run-off from eroding continents and increased upwelling along ocean basin margins.

Increased rates of aerobic photosynthesis mean increased rates of 0_2 production and, for the first time, rates of 0_2 *production* may have exceeded those of 0_2 *consumption,* resulting in the accumulation of free 0_2 (>1% PAL) in the atmosphere. The final consequence of this biota/crust/atmosphere interaction would be the evolution of aerobic respirers. Note that this interpretation does not require that physiologically modern cyanobacteria evolve just prior to the build-up of atmospheric oxygen, although two versions of that scenario have been advanced by Cloud (1976) and Schopf (1978). A fuller treatment of the Archean/Proterozoic transition and its probable ecological consequences can be found in Knoll (1979).

The best microfossil evidence of Early Proterozoic life comes not from Africa, but rather from North America where two distinctive types of microbiotas are known. Most famous is the biota of the 2 000 m.y. old Gunflint Iron Formation described by Barghoorn & Tyler (1965). Stromatolitic Gunflint assemblages are overwhelmingly dominated by simple spheroids and thin filamentous sheaths, with a dozen or more problematic bacteria of diverse morphologies scattered throughout the cherts. More distal facies contain a non-stromatolitic benthos dominated by the *Metallogenium*-like trichospheric bacterium *Eoastrion* Barghoorn, as well as populations of large spheroidal unicells interpreted as plankton (Knoll *et al.*, 1978). The silicified coastal carbonates of the Belcher Supergroup, eastern Hudson Bay, contain few, if any, taxa in common with the Gunflint. Instead, a Bitter Springs-like biota of diverse, morphologically modern blue-greens is found (Hofmann, 1976). The recent discovery of a new Gunflint-like microbiota in the Sokoman Iron Formation of northeastern Quebec confirms the hypothesis that the Gunflint and Belcher types of biotas lived contemporaneously in different environments (Knoll & Simonson, 1981). Gunflint biotas seem to have thrived in habitats where sedimentary iron deposition was possible (this does not carry the implication that the organisms were directly responsible for iron precipitation), whereas Belcher communities inhabited sabkha-like environments, much as their morphologic counterparts do today (Golubic & Hofmann, 1976). Early Proterozoic microfossils have been described from Transvaal carbonates (Nagy, 1974, 1978; Macgregor *et al.*, 1974); however, recent investigations have opened the possibility that at last some of these remains may be endolithic microbes that are much younger than the rocks in which they are found (Hofmann, in press). Thin (cm scale) but remarkably persistent horizons of organic matter found in Witwatersrand sequences also contain microstructures of probable biological origin (Hallbauer & Van Warmelo, 1974; Hallbauer, 1975).

THE LATE PROTEROZOIC

The major biological events of the Late Proterozoic Era were the evolution of the eukaryotic cell and the origin of multicellular plants and animals. Surprisingly, relatively little of the critical evidence bearing on the timing and consequences of these events comes from African rocks. I say 'surprisingly', because the *potential* for major African contributions to our understanding of both events is great.

Stromatolites abound in late Precambrian carbonates of Africa, and many of these have been well described, especially those in the northwestern part of the continent (*e.g.,* Bertrand-Sarfati, 1972a, b; Fig. 3.3). These structures indicate that through the end of the Proterozoic (and in many places well into the Paleozoic), cyanobacterial mats continued to form wherever bottom conditions permitted, even in the face of radiating eukaryotes and, later, metazoans. A few somewhat sketchy reports of stromatolitic microbiotas have been published (e.g., Boureau, 1975, 1976; Edhorn, 1978), but these fossils tell us little in comparison to the beautifully preserved microfloras of Australia (Schopf, 1968; Schopf & Blacic, 1971; Oehler, 1978) and Svalbard (Knoll, 1982, Fig. 2.5 & 3.4–3.6). Descriptions of organic walled acritarchs (presumed planktonic cells of uncertain systematic position) from detrital facies are likewise few in number and limited in content (Binda, 1972; Lopukhin *et al.*, 1974; Choubert *et al.*, 1979; and others).

From sequences in other parts of the world, principally Scandinavia, the Soviet Union and, increasingly, North America, a picture of eukaryotic cell evolution has begun to emerge. Large, robust walled acritarchs (Fig. 3.1 & 3.2) are common in open marine siltstones and shales younger than about 1 400 m.y., but are extremely rare or absent in similar older rocks (Schopf & Oehler, 1976). The implication is that this striking change in the Precambrian fossil record may record the appearance of fossilizable nucleated cells in marine ecosystems. Relatively little is known about early acritarch assemblages, but sequences spanning the interval from 1 000 m.y. to the base of the Cambrian have been well studied (e.g., Vidal, 1976), and these yield a consistent picture of increasing structural diversity among acritarchs, interpreted as a late Precambrian radiation of eukaryotic phytoplankton (Vidal & Knoll, 1983). Curiously, nucleated cells seem to have come to dominate the planktonic realm long before they displaced cyanobacterial communities from shallow benthonic niches. More curious, it is clear that the plankton biota suffered major extinctions at the end of the Precambrian, roughly coincident in time with the widespread deposition of glaciogenic sediments (Vidal & Knoll, 1983). Latest Precambrian acritarch assemblages are remarkably depauperate relative to biotas 100 m.y. older; plankton diversity didn't recover until the radiation of morphologically microplankters in early Cambrian times.

Most of the late Precambrian microfossil record consists of algae and cyanobacteria, but in rocks 750

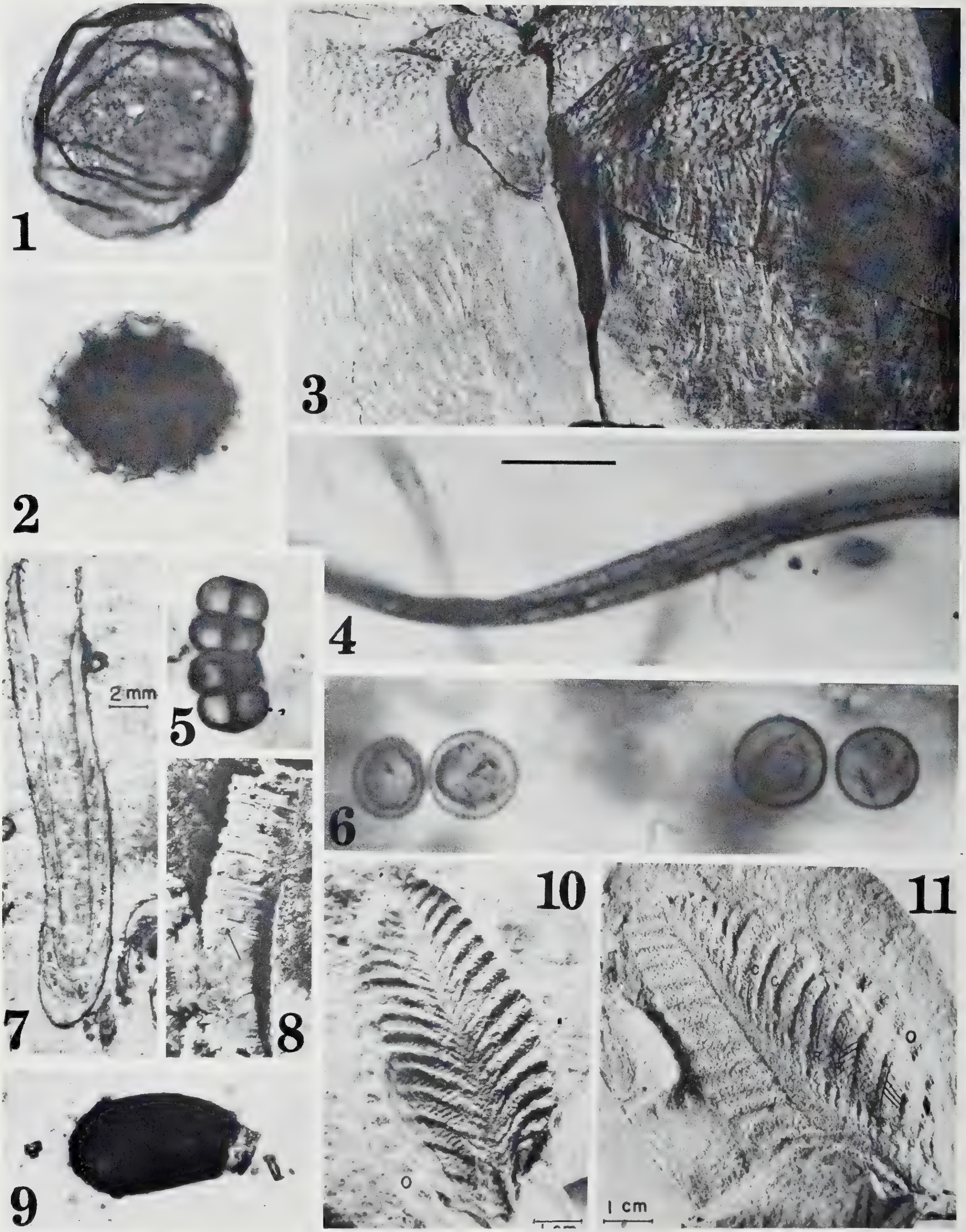

FIG. 3. — Late Precambrian stromatolites, microfossils, and macrofossils. Bar in Fig. 3.4 = 20 µm for 1 and 2, 20 cm for 3, 13 µm for 4–6, 6 mm for 7 and 8, 50 µm for 9, and 18 mm for 10 and 11.
1, *Kildinella* sp. A Vidal from the Andersby Formation, East Finnmark, northern Norway; 2, *Vandalosphaeridium reticulatum* (Vidal) Vidal from the Visingsö Beds, Sweden; 3, bioherm of columnar stromatolites from the Atar Group, Mauritania; 4, *Eomycetopsis robusta* Schopf em. Knoll and Golubic, the preserved sheath of a mat building oscillatorian cyanobacterium, from the Late Precambrian Draken Formation, Svalbard; 5, *Sphaerophycus wilsonii* Knoll, a mat dwelling cyanobacterium from the Draken Formation; 6, *Gloeodiniopsis gregaria* Knoll and Golubic from the Draken Formation; 7 & 8, thin section and surface views of *Cloudina hartmannae* Germs, a calcareous Metazoan tube from the Kuibis Formation, Nama Group, South West Africa (Namibia); 9, vase-shaped test of a heterotrophic protist from the Backlundtoppen Formation, Svalbard; 10 & 11, natural mold and latex cast of *Rangea schneiderhoehni* Gürich, an early coelenterate from the Kuibis Formation, Nama Group, South West Africa/Nambia. Figs 1 & 2 courtesy of G. Vidal; 3, courtesy of J. Sarfati and by permission of Elsevier Publishing Company, 7, 8, 10, & 11, courtesy of G. J. B. Germs.

to 650 m.y. in age, vase-shaped, organic tests of heterotrophic protists are being found with increasing frequency. First discovered in shales from the Grand Canyon, U.S.A. (Bloeser *et al.*, 1977), these distinctive fossils have now been found in Sweden, East Greenland, Svalbard, Brazil, and Saudi Arabia (Fig. 3.9). Biostratigraphically, they appear to be excellent index fossils, and ecologically, they provide evidence for the increasing complexity of marine ecosystems (Knoll & Vidal, 1980).

In latest Precambrian (approximately 650–590 m.y.). sedimentary sequences of Australia, Eurasia, and North America, casts and molds of simple, soft-bodied invertebrates document the initial evolution of metazoans, some of them coelomate. Among the foremost of these 'Ediacaran' invertebrate faunas is a beautifully preserved biota from the Nama Group, South West Africa/Namibia. Here abundant casts of pennatulid coelenterates (Fig. 3.10 & 3.11) are found, in addition to medusoids, a possible annelid worm, and calcareous worm tubes (Fig. 3.7 & 3.8) that constitute some of the earliest evidence for Metazoan biomineralization (Gürich, 1930; Germs, 1972a, 1973; Glaessner, 1979; Pflug, 1970). Associated trace fossils preserve the behavioral patterns of early deposit feeders (Germs, 1972b).

Early metaphytes are unknown from the African continent, but abundant ribbon-like algae up to 1 cm wide do occur in latest Precambrian shales of Eurasia (Gnilovskaya, 1971). The oldest morphologically regular carbonaceous macrofossils yet unearthed are cm-scale ellipsoidal to elongated bodies assigned to the species *Tawuia dalensis* Hofmann and Aitken, 1979. First found in shales thought to be approximately 850 m.y. old in northwestern Canada, these distinctive problematica have recently been discovered in contemporaneous strata in China and Svalbard. Intriguingly, populations of *T. dalensis* exhibit allometric growth patterns, suggesting a well integrated body plan. Whether they represent extremely regular algae or ancestral flatworm like metazoa is unknown; however, this may be resolvable by careful organic geochemical analysis. If animal, these fossils would extend in time an evolutionary transition to integrated multicellularity that at present must be viewed as extremely rapid.

Unmetamorphosed late Precambrian sedimentary sequences are widespread in Africa. Detrital accumulations of the Awat series in Egypt; clastics and carbonates from the Hoggar, Anti-Atlas, Adrar and many other areas of north-western Africa; glaciogenic and other clastic formations from Sierra Leone and Ghana; lithologically heterogeneous rocks extending in an arcuate pattern from the north-western Cape Province through Angola and into Zaire and Zambia — all of these sequences and several others are likely to contain critical evidence allowing paleontologists to test, refine and augment the ideas and evidence outlined in the above paragraphs.

In summary, Precambrian organic evolution can be viewed as a series of steps connecting successive biologic plateaus. Radiations triggered by evolutionary innovations and/or major shifts in the physical environment were probably rapid, whereas ensuing periods prior to subsequent radiations were likely characterized by the biological fine-tuning of communities. In general, radiations resulted in increased ecosystem complexity through the addition of new taxa, rather than in the extinction and replacement of antecedent organisms (Knoll & Awramik, 1983). African rocks and fossils, and of course African geologists, have been fundamental in shaping ideas on early evolution, and it is likely that the late Precambrian sedimentary sequences of the continent will turn out to be as important to our growing knowledge of early eukaryote, metazoan, and metaphyte biology as the early Precambrian strata of southern Africa have been for Archean evolution.

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Vascular plants from the Devonian to Lower Cretaceous in southern Africa

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ABSTRACT

The succession of pre-angiospermous megafloras in southern Africa from the Devonian to Lower Cretaceous is outlined. Interrelationships between continental drift, global climatic trends, and floral and faunal evolution are emphasized. Data are given on numbers of assemblages sampled; on species diversity; and on relative abundance of each genus per productive 'formation'. A total of 79 genera and about 250 species are recognized in the 150 assemblages from the 11 horizons considered. Floras are unknown from the Carboniferous and are as yet undescribed from the Jurassic. Aside from these gaps, a good idea of the floral development is obtained. Diversity lows of around 5 to 10 species per 'formation' are witnessed in the Devonian, whereas a peak of 112 species is encountered in the Upper Triassic Molteno Formation. Diversity remains around 20 to 30 species for all other 'formations'.

RÉSUMÈ

LES PLANTES VASCULAIRES DE LA PÉRIODE ALLANT DU DÉVONIEN AU CRÉTACÉ INFÉRIEUR, EN AFRIQUE DU SUD

La succession des mégaflores pré-angiospermes en Afrique du Sud du Dévonien au Crétacé inférieur est esquissée. Les relations entre la dérive des continents, les tendances climatiques globales et l'évolution de la flore et de la faune sont soulignées. Des informations sont données sur les nombres d'assemblages échantillonnés, sur la diversité des espèces, et sur l'abondance relative de chaque genre par 'formation' productive. Un total de 79 genres et environ 250 espèces sont reconnu dans les 150 assemblages des 11 horizons considérés. Les flores ne sont pas connues à partir du Carbonifère et ne sont pas encore décrites à partir du Jurassique. À part ces lacunes, une bonne idée du développement des flores est obtenue. Des normes de diversité d'environ 5 à 10 espèces par 'formation' sont observées dans le Dévonien tandis qu' un maximum de 112 espèces recontré dans la Formation Molteno du Triassique supérieur. La diversité demeure autour de 20 à 30 espèces pour toutes les autres 'formations'.

INTRODUCTION

This brief history of vascular plants, as seen particularly in South Africa, from their late Silurian origin to the rise to dominance of the angiosperms in the mid-Cretaceous, was first presented in embryo form at the AETFAT Congress in January 1982.

In order to fill out the story, which can only be partially pieced together from the current literature, we have since examined all the relevant collections housed in South Africa. It became evident also that certain formations needed to be further collected. We have organized several field trips to sample the Devonian Witteberg and Bokkeveld Groups, the Lower Triassic Burgersdorp formation, and the Lower Cretaceous Kirkwood Formation and equivalents. We have also drawn on the unpublished information of fellow palaeobotanists.

While undertaking this additional work, we decided to expand the contribution into a full Prodromus of the megaplants of South Africa from the Devonian to Lower Cretaceous. This has become a 300-page monograph, including a 150-page photographic catalogue of all taxa encountered; a taxonomic review of all forms; locality maps and discussion of the depositional environment of each formation; and biographical sketches of collectors. The Prodromus should be available soon after publication of the Congress Proceedings.

We are personally involved in a revision of the palaeoflora of the Molteno Formation, by far the richest horizon in number of localities and diversity of plants in South Africa. The first volume of that work, which includes a résumé of the whole flora, has been recently published. The Prodromus draws on this Molteno work but does not repeat the details.

The present paper is essentially a summary of the Prodromus. References are therefore excluded. Since the paper had to go to press before completion of the Prodromus, a few details will inevitably be altered in the later expanded version.

GLOBAL ENVIRONMENTAL TRENDS

First, we will consider very briefly the major global trends witnessed during the 300 million year interval with which we are concerned. This forms the backdrop to our story.

Continental drift

Over the past half billion years (500 million years) three clear phases of continental drift are discerned: the first in which a number of separate continents occur which are seen to be converging on one another; the second during which a single relatively stable supercontinent (Pangaea) exists; the third in which we witness the fragmentation of Pangaea and the drifting apart of newly delineated continents. Our 300 million year interval of plant evolution covers the latter part of phase one, the whole of the Pangaeic phase and the initial stages of fragmentation leading to phase three.

Global climatic trends

Equally dramatic climatic shifts are witnessed. Average global temperatures and precipitation have

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varied considerably. Very broadly the trend has been from medium temperatures and precipitation in the late Silurian; through to an extreme cold wet peak in the latter half of the Carboniferous with the development of extensive polar ice caps particularly in the south; followed by a long interval with the steady growth of ever warmer and drier conditions through to the Middle Cretaceous; from which time the trend was reversed till the present when polar caps once again exist.

It is a very significant fact that polar ice caps are a rarity rather than the norm in earth history. Only during such glacial intervals (e.g. later Carboniferous and the present) are global climatic belts strongly differentiated.

Global floras

The history of vascular plants is characterized by a succession of mass extinctions and evolutionary bursts. First in the succession came the psilophytes; then appeared the lycopods, horsetails and ferns; followed shortly after by the seed ferns (pteridosperms); from which probably arose the conifers, ginkgos and cycads and the now extinct bennettitaleans; and lastly, the highly successful flowering plants.

Global faunas

The animal world follows a parallel interdependent pattern of extinctions and radiations. The early amphibians and reptiles coincide approximately with the early pteridopytes; the mammal-like reptiles with the seed-ferns; the dinosaurus with the conifers, cycads and ginkgos; and finally, the birds and mammals with the flowering plants.

PRESERVATION AND SAMPLING OF PALAEOFLORAS IN SOUTHERN AFRICA

The evolutionary history of the vascular plants is pieced together from the differently preserved dissociated plant organs. Leaves, fruit and seeds, and certain stems are usually preserved as impressions in pale fine-grained sediments, more rarely as compressions with cuticle preserved in fine carbonaceous sediments. Pollen and spores occur by the millions as resistent cuticular coatings in carbonaceous sediments. Silicified stems occur in sandy sediments.

The table, figures and text presented here are based essentially on the first category, the foliage, reproductive structures and certain stem impressions. These have been most comprehensively sampled and studied.

Although this paper discusses southern Africa (taken here as Africa south of the Sahara), in general the story is essentially told on the basis of South African material. In each successive geological period by far the most frequently preserved, best sampled and most fully studied assemblages are from South Africa. Only in the Permian are relatively good occurrences known elsewhere in southern Africa.

Since southern Africa fell entirely within the Gondwana plant realm during the 300 million year interval discussed, and since floras during each period are broadly similar throughout the realm, we feel justified in basing our story on the South African material.

The collection of fossil plants in South Africa has been underway now for around 150 years. Amateurs and professionals alike have made their contribution. The outline of developing floras and the statistics on diversity presented, can probably be taken as reasonably comprehensive. In reading the following synopsis, refer to Table 1 and Figs 1 & 2.

SILURIAN (440–400 m. yrs)

Global geography

During this period the massive southern supercontinent Gondwana lay virtually entirely S. of 30°S, with the south pole situated approximately in today's Angola. A smaller Euramerican continent lay in the equatorial belt, with a 1 500 km arm of sea isolating it from Gondwana. A few minor 'Asian' landmasses lay further afield.

No ice caps adorned the polar regions. Global climates were equable with relatively weak differentiation of climatic belts. Temperatures and precipitation were of medium proportions.

Global flora

The vascular plants made their earliest appearance in the late Silurian (close on 400 million years ago) of the Euramerican equatorial belt. They are known from Wales, Czechoslovakia, New York State and W. Russia. These earliest pioneers, referred to the Psilophyta, were small, simple, little differentiated, homosporous, vascular plants with dichotomous branching, but with no leaves and no roots.

Southern African strata

Sediments of Silurian age are unknown in Africa south of the Sahara.

Southern African flora

The Gondwana landscape was entirely barren of vascular plant life at this period.

DEVONIAN (400–360 m. yrs)

Global geography

During the Devonian Gondwana drifted northwards, steadily narrowing the seaway between its northern shores and Euramerica. The latter remained more or less static in its tropical domain. The southern pole was, towards the close of the period, situated possibly in today's South West Africa/Namibia. Global climates remained much the same as during the Silurian, with the polar regions still devoid of ice caps.

Global flora

The Devonian saw the spread and diversification of vascular plant life with all landmasses becoming colonized. In the earlier Devonian we witness a dwarf vegetation. Nothing grew over a metre or so in height and psilophytes dominated. Floras throughout the world at this time were very similar, there being little evidence of provincialism. By the close of the Devonian more diverse communities, still of a

TABLE 1.— South African palaeofloras, sampling, diversity and relative abundance

	Bokkeveld	L-M Witteberg	U Witteberg	L Ecca	M Ecca	U Ecca	Estcourt	Burgersdorp	Molteno	Drakensberg	Kirkwood
BRYOPHYTA											
Buthelezia	-	-	-	-	-	-	1	-	-	-	-
Muscites	-	-	-	-	-	-	-	-	2	-	-
HEPATOPHYTA											
Marchantites	-	-	-	-	-	-	-	-	2	-	1
cf. Riccia	-	-	-	-	-	-	-	-	-	-	1
PSILOPHYTA											
Palaeostigma	3	4	-	-	-	-	-	-	-	-	-
Dutoitii	5	4	-	-	-	-	-	-	-	-	-
LYCOPHYTA											
cf. Zosterophyllum	3	-	-	-	-	-	-	-	-	-	-
Haplostigma	3	5	-	-	-	-	-	-	-	-	-
Archaeosiggilaria	4	3	5	-	-	-	-	-	-	-	-
Leptophloeum	-	4	-	-	-	-	-	-	-	-	-
Drepanophycus	-	2	2	-	-	-	-	-	-	-	-
cf. Haplostigma	-	-	-	4	-	-	-	-	-	-	-
cf. Leptophloeum	-	-	-	5	-	-	-	-	-	-	-
Cyclodendron	-	-	-	-	4	-	-	-	-	-	-
Lycopodiopsis	-	-	-	-	4	-	-	-	-	-	-
incertae sedis	-	-	-	-	-	-	-	1	-	-	-
SPHENOPHYTA											
Annularia	-	-	-	-	1	2	-	-	-	-	-
Sphenophyllum	-	-	-	-	2	1	3	-	-	-	-
Raniganjia	-	-	-	-	-	2	2	-	-	-	-
Paracalamites	-	-	-	-	-	-	4	-	-	-	-
Phyllotheca	-	-	-	-	-	-	3	-	2	-	-
Schizoneura	-	-	-	-	-	-	2	-	2	-	-
Neocalamites	-	-	-	-	-	-	-	5	4	-	-
Equisetites	-	-	-	-	-	-	-	-	1	✓	-
FILICOPHYTA											
Calamophyton	-	1	-	-	-	-	-	-	-	-	-
Pecopteris	-	-	-	-	2	-	-	-	-	-	-
Sphenopteris	-	-	-	-	1	1	2	-	-	-	2
Cladophlebis	-	-	-	-	-	-	-	-	2	-	3
Todites	-	-	-	-	-	-	-	-	2	-	-
Asterotheca	-	-	-	-	-	-	-	-	3	-	-
Dictyophyllum	-	-	-	-	-	-	-	-	1	-	-
incertae sedis	-	-	-	-	-	-	-	1	-	-	-
INCERTAE SEDIS											
foliage gen. A	-	-	-	-	-	-	1	-	-	-	-
" gen. B	-	-	-	-	-	-	-	-	1	-	-
" gen. C	-	-	-	-	-	-	-	-	1	-	-
Drepanozamites	-	-	-	-	-	-	-	-	1	-	-
foliage gen. D	-	-	-	-	-	-	-	-	1	-	-
Kurtziana	-	-	-	-	-	-	-	-	2	-	-
Pachypteris	-	-	-	-	-	-	-	-	1	-	-
Ginkgophytopsis	-	-	-	-	-	-	-	-	2	-	-
Chiropteris	-	-	-	-	-	-	-	-	1	-	-
Onychiopsis	-	-	-	-	-	-	-	-	-	-	4
PROGYMNOSPERMS											
Platyphyllum	-	1	-	-	-	-	-	-	-	-	-
twig gen. A	-	1	-	-	-	-	-	-	-	-	-
" gen. B	1	-	3	-	-	-	-	-	-	-	-
" gen. C	-	-	4	-	-	-	-	-	-	-	-
PTERIDOSPERMS											
Gondwanidium	-	-	-	-	3	-	-	-	-	-	-
Gangamopteris	-	-	-	-	2	-	-	-	-	-	-
Palaeovittaria	-	-	-	-	2	-	-	-	-	-	-
Glossopteris	-	-	-	-	5	5	5	-	2	-	-
Dicroidium	-	-	-	-	-	-	-	5	5	-	-
Lepidopteris	-	-	-	-	-	-	-	4	3	-	-
INCERTAE SEDIS											
Taeniopteris	-	-	-	-	2	-	1	-	3	-	2
Yabeiella	-	-	-	-	-	-	-	-	3	-	-
Dejerseya	-	-	-	-	-	-	-	-	2	-	-
Saportaea	-	-	-	-	-	-	-	-	1	-	-
Linguifolium	-	-	-	-	-	-	-	-	1	-	-
foliage gen. D	-	-	-	-	-	-	-	-	1	-	-
" gen. E	-	-	-	-	-	-	-	-	1	-	-
CONIFERALES											
Walkomiella	-	-	-	-	2	-	-	-	-	-	-
foliage shoot gen. A	-	-	-	-	2	-	-	-	-	-	-
Noeggerathiopsis	-	-	-	-	4	3	2	-	-	-	-
foliage shoot gen. B	-	-	-	-	-	-	2	-	-	-	-
Rissikia	-	-	-	-	-	-	-	-	3	-	-
Heidiphyllum	-	-	-	-	-	-	-	-	5	-	-
foliage shoot gen. C	-	-	-	-	-	-	-	-	-	✓	-
Taxites	-	-	-	-	-	-	-	-	-	-	2
Brachyphyllum	-	-	-	-	-	-	-	-	-	-	3
GINKGOALES											
Psygmophyllum	-	-	-	-	1	-	-	-	-	-	-
cf. Nephropsis	-	-	-	-	1	-	-	-	-	-	-
cf. Phoenicopsis	-	-	-	-	1	-	-	-	-	-	-
Ginkgoites	-	-	-	-	1	-	-	1	3	-	-
Baiera	-	-	-	-	-	-	-	2	4	-	-
CYCADALES											
Pseudoctenis	-	-	-	-	-	-	-	3	3	-	-
Nilssoniopteris	-	-	-	-	-	-	-	-	1	-	-
BENNETTITALES											
Otozamites	-	-	-	-	-	-	-	-	-	✓	-
Zamites	-	-	-	-	-	-	-	-	-	-	5
Pterophyllum	-	-	-	-	-	-	-	-	-	-	3
Dictyozamites	-	-	-	-	-	-	-	-	-	-	2

GENERA INCLUDED

a. Foliage genera.
b. Stem impressions of plants not represented by foliage.
c. The mosses and liverworts, although not vascular plants, are included for completeness, since they occur in the same assemblages as the rest.

Fruit, seeds and silicified wood are excluded since their inclusion would amount to duplication of natural taxa. The aim here is to show diversity and relative abundance of natural taxa making up the communities of the deltas, swamps, river systems etc. of the periods in question.

GENERIC NAMES

The generic names applied here are those available in the most recent literature. Certain names will be altered, and unnamed genera formally described, in the Prodromus Volume mentioned in the Introduction. That volume will also include photographs illustrating all taxa; as well as more precise abundance and frequency data.

GEOLOGICAL HORIZONS

As included in Figs 1 & 2.

KEY

✓	present
1	very rare
2	rare
3	intermediate
4	common
5	dominant

65 m. yrs.

Period	Geological formation or group	Assemblages (Mini assemblage)	(Total genera) Total species	Max. species per assemblage	Average species per assemblage
CRETACEOUS 140	Kirkwood	14(-)	(11)28	7	4
JURASSIC 200	Drakensberg	?	?	?	?
TRIASSIC	Molteno	67(-)	(34)112	62	10
245	Burgersdorp	13(21)	(8)18	15	4
PERMIAN	Estcourt	24(-)	(12)22	13	5
	U Ecca	2(-)	(6)16	9	7
	M Ecca	10(-)	(18)32	23	12
300	L Ecca	2(1)	(2) 2	2	2
CARBONIF. 360					
DEVONIAN	U Witteberg	9(5)	(4) 4	3	2
	L-M Witteberg	6(8)	(9)12	4	2
400	Bokkeveld	3(3)	(6) 6	2	1
SILURIAN 440					

PRODUCTIVE HORIZONS

The geological horizons listed are all those in South Africa yielding useful and distinctive foliage (& stem impression) assemblages. Their rough positions within the geological periods are indicated.

ASSEMBLAGES

a. An assemblage is a collection of fossils from a distinct rock unit of restricted area and stratigraphical extent (lithosome).
b. An assemblage will generally represent the plants growing in the relatively near vicinity of the river channel, lake or swamp in which the fossiliferous deposit accumulated.
c. In the most productive, comprehensively sampled horizons (e.g. the Middle Ecca, Estcourt and Molteno formations) only those assemblages represented by numerous specimens have been considered.
d. In the least productive horizons (e.g. Bokkeveld, Witteberg and Burgersdorp), assemblages with down to 5 recognisable specimens are included. Mini-assemblages, with 1—4 specimens, are also taken note of to fill out the flora.
e. Assemblages have been collected from sedimentary pockets within the Drakensberg lavas. The material is housed in France and data for this table is not yet available. We hope that it will be so for the Prodromus (see Introduction).

DIVERSITY

a. Species diversity in a few instances includes infra-specific taxa.
b. We have for this work studied all relevant collections around the country. The statistics represent our own assessment of taxonomy, thus achieving a measure of internal consistency.

cosmopolitan nature, including larger trees, had evolved. Psilophytes, lycopods, ferns and progymnosperms were all in evidence.

Southern African strata.

The only known Devonian rocks in southern Africa outcrop along the southern Cape fold mountain belt and down the Natal and Transkei coastal region. Relatively narrow seaways occupied these now elevated stretches of country. A series of rivers disgorged sediments into the basins with a number of deltas forming. The Bokkeveld and Witteberg Group sediments (shales, siltstones and sandstones) of Middle and Upper Devonian age resulted.

South African flora

It is the plants of the communities occupying the river banks, flood plains and marshes of the deltas that were occasionally preserved. Fossil plant localities are infrequent. Only from a handful of localities can large well preserved collections be assembled, whilst the material is more normally found as isolated specimens or fragmentary debris. A total of 12 genera and 15 species of psilophytes, lycopods, a possible fern and a few possible progymnosperms are known. The floras were clearly dominated both in diversity and abundance by the lycopods which occur as stem casts and moulds. Assemblages are invariably of very limited diversity (maximum 3 species, average 2 species.)

Silicified stems and cuticular material remain unknown. The strata, having been subjected to intense folding and metamorphism, are unsuitable for spore and pollen preservation.

CARBONIFEROUS (360–300 m. yrs)

Global geography

The Gondwana supercontinent continued to drift northwards through the Carboniferous. Collision with Euramerica occurred around the middle of the period.

This had a profound effect on world climates. The ocean currents were radically redirected, the warm waters of the west flowing equatorial current being deflected north and south to high latitudes. With abnormal levels of evaporation at high latitude and consequent precipitation in the form of snow, an extensive ice cap of proportions like Antarctica today gradually built up. The ice covered the southern third of Gondwana, including all of southern Africa, which lay beyond 60°S. Simultaneously, copious rains fell along the steamy equatorial belt. Marked climatic belts developed.

Global flora

While southern Africa lay fallow beneath the ice, tropical Euramerica experienced perhaps the longest, wettest deluge in earth history. Extensive wet forest and swamp vegetation spread. Lycopods, sphenophytes, ferns and seed ferns were now co-dominants. The major coal deposits of the USA and Europe owe their origin to this tropical biomass explosion.

Southern African strata

Sediments of Carboniferous age remain unproven in Africa south of the Sahara.

PERMIAN (300–245 m. yrs)

Global geography

By the Permian the single supercontinent Pangaea had fully welded together and straddled the globe from North to South Poles. Much of Pangaea had shifted markedly northwards such that less of Gondwana lay within the Antarctic Circle. By the close of the Permian southern Africa stretched from 30° to 60°S with South Africa at 50° to 60°S.

The northerly shift, together with relatively minor changes in continental configuration, appears to have resulted in further dramatic climatic changes. The southern ice cap waned and disappeared in the Lower Permian. The water released by the melting ice flooded all low lying landscape. However, through the remainder of the Permian with the continued inward radial drive of the tectonic plates, Pangaea buckled upwards, and was steadily drained of all its shallow seas. The vast interior of the global continent became desertified.

Global flora

During the Permian four distinctive plant realms developed: Gondwana, Euramerica, Cathaysia, Angara. The Gondwana Realm occupied the greater part of Gondwana, and stretched from 30°S to 90°S with remarkably uniform communities growing throughout. Pteridophyta, and particularly the lycopods, were dominant during the early phase of flooding after the retreat of ice. The seed fern *Glossopteris* soon took over and became the overwhelmingly dominant and most diverse genus through most of the Permian throughout the realm. It was fully contained within the realm.

With the complete draining of the shelf seas and the massive desertification late in the Permian, marine and freshwater invertebrates were decimated as were the terrestrial plants and animals.

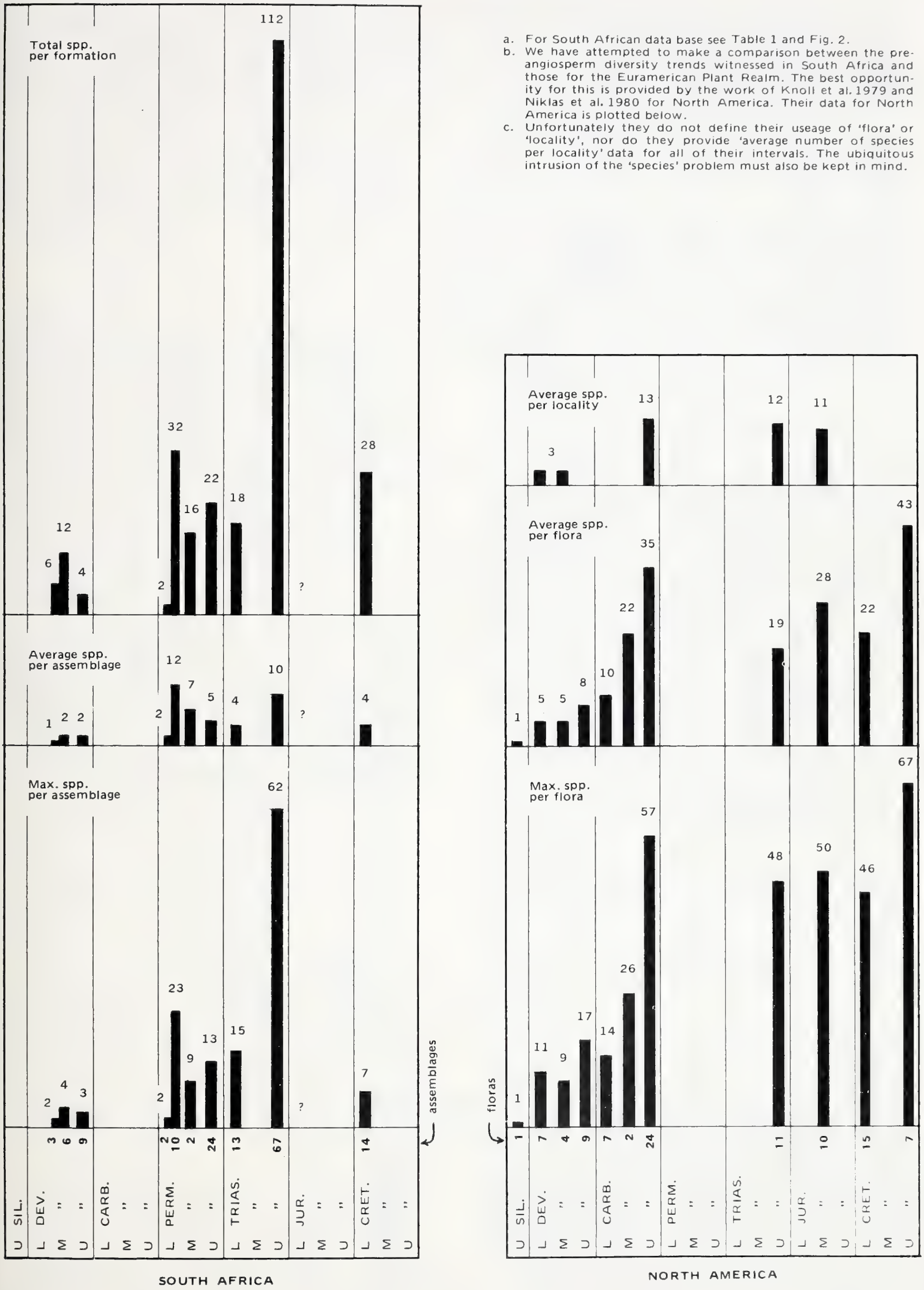
Southern African strata

The southern Africa which emerged after the retreat of the ice was significantly different from that which we saw during the Devonian, before the onset of the ice age. Basins and rifts galore appeared throughout the sub-continent. The succession of strata which filled these features — tillites, shales and coals, red muds and silts — is everywhere remarkably similar.

Southern African flora

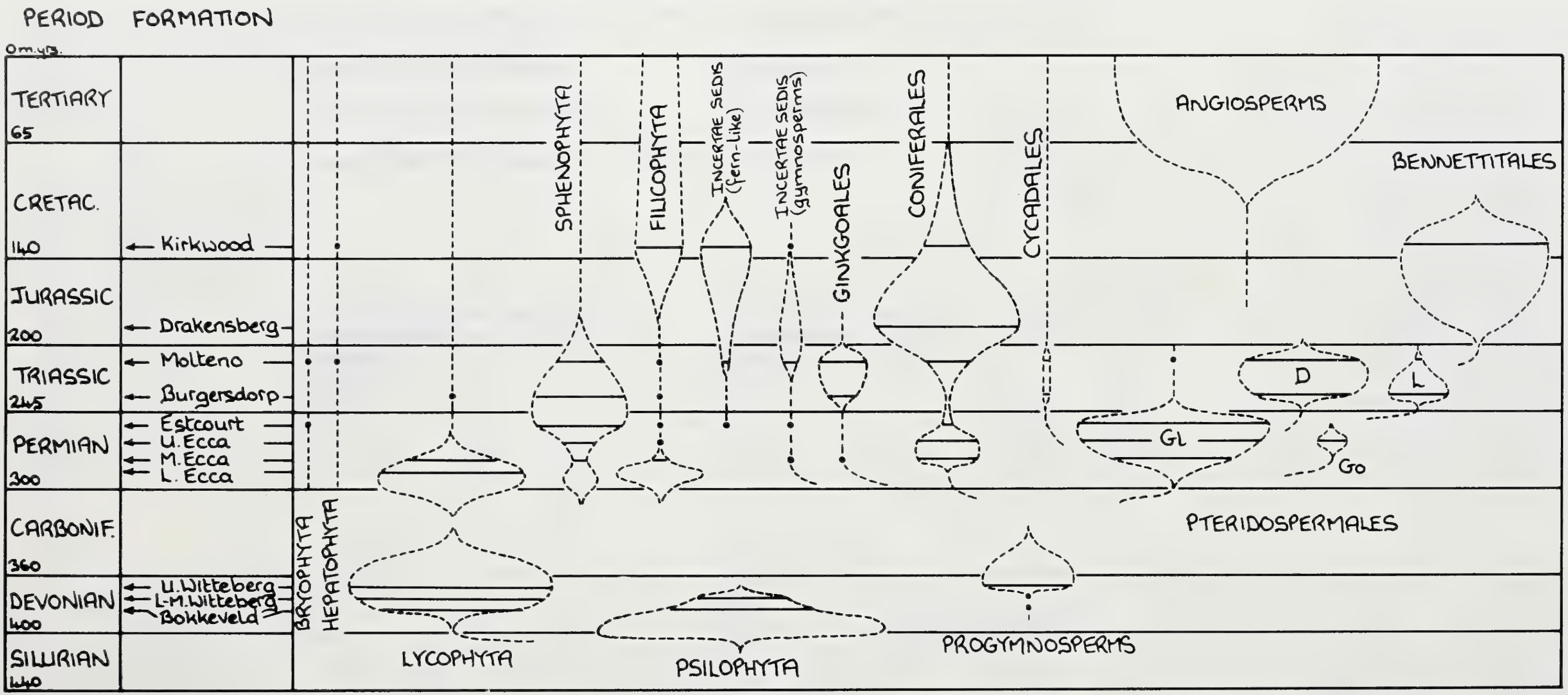
The Permian period is unique in a number of respects. It is the only period for which a number of good megaplant assemblages are known to the north of South Africa. It includes, also, a greater number of productive horizons than any other period. It is in the Middle Ecca and equivalents of the Lower Permian that the vast coal reserves of the region occur.

Diversity reached distinctly higher levels in the Permian than in the Devonian. The Lower Permian



a. For South African data base see Table 1 and Fig. 2.
b. We have attempted to make a comparison between the pre-angiosperm diversity trends witnessed in South Africa and those for the Euramerican Plant Realm. The best opportunity for this is provided by the work of Knoll et al. 1979 and Niklas et al. 1980 for North America. Their data for North America is plotted below.
c. Unfortunately they do not define their useage of 'flora' or 'locality', nor do they provide 'average number of species per locality' data for all of their intervals. The ubiquitous intrusion of the 'species' problem must also be kept in mind.

FIG. 1.—Diversity trends in pre-angiosperm fossil floras.



a. The figure is based directly on the South African data as presented in Fig. 1.
b. The balloons are drawn to scale to faithfully reflect observed relative abundance.
c. The vertical axis is also to scale, showing relative duration of the geological periods.

Gl — Glossopteris
Go — Gondwanidium
D — Dicroidium
L — Lepidopteris
1 mm (horiz.) — 2% of total flora
● — 1% or less of total flora
broken line — presumed occurrence

FIG. 2.—Evolution of vascular plants in South Africa.

coal measure flora consists of 18 genera and 32 species. After the initial short ascendent spell enjoyed by the lycopods, *Glossopteris* rose to dominance and maintained that role for a clear 30 million years. The sphenophyta steadily increased in significance throughout the Permian.

Good spore and pollen assemblages have been studied through a fairly complete Permian sequence both in South Africa and further north. These support and elaborate on the megaflora evidence in piecing together the patterns of floral history.

TRIASSIC (245–200 m. yrs)

Global geography

Pangaea appears much the same in shape and latitudinal position as it did during the Permian. The Permian/Triassic (Palaeozoic/Mesozoic) transition marked the turning point in the cycle of continental drift. From this time on the tectonic plates ceased their inward radial drive. There followed rebound and outward drift through till the present. Pangaea subsided in the Lower Triassic and all low-lying country was once again flooded.

The vast interior remained desertified. In the absence of polar ice caps latitudinal climatic belts were little differentiated.

Global flora

After the decimation of plant and animal life at the close of the Permian, a major shift in prominence of plant classes occurred. The pteridophytes were displaced by the gymnosperms. Ginkgos, conifers, cycads, bennettitaleans and new orders of seed fern became pre-eminent. During the early Triassic global flooding of low country, extensive low diversity lycopod groves spread (much as witnessed during the flooding in the early Permian). This was the swansong of the lycopods. With the general trend towards warmer drier climates through the Triassic, and indeed through the whole Mesozoic, the more diverse gymnosperm communities took hold.

Southern African strata

In southern Africa deposition occurred in rejuvenated Permian basins and rifts. Lacustrine, riverine and floodplain deposits accumulated intermittently through the Triassic. We visualize the highly fossiliferous Molteno Formation as being deposited in a situation not unlike the Okavango Swamps in Botswana: with rivers flowing inland and terminating in an extensive swampy depression bordering the desertic Gondwana interior.

Southern African flora

Although scattered megaplant occurrences are known elsewhere in southern Africa, by far the most productive deposits are confined to the Karoo Basin of South Africa. The Upper Triassic Molteno ranks as easily the most productive megaplant yielding formation of any age in South Africa. In total diversity (112 species), its flora is three to four times richer than the next most lucrative formation — the Middle Ecca with 32 species. The Molteno Formation is relatively carbonaceous in character (with minor coal deposits) and, as such, also yields excellent spore and pollen assemblages.

The Lower-Middle Triassic Burgersdorp Formation, the only other productive horizon of the period in South Africa, is altogether different. It is characterized by purple, green and buff coloured sediments and is primarily tetrapod (bone) bearing. Foliage and stem impressions occur only in the silty sandstones.

The Gondwana Triassic plant realm, including South Africa, follows the global pattern in that a wide range of gymnospermous plants, ginkgos, cycads, conifers and seed ferns, are prominent. As with *Glossopteris* in the Permian, *Dicroidium* (also a seed fern) was by far the most abundant, ubiquitous, diverse plant through most of the Triassic (some 30 m. yrs) throughout the realm. Also, like *Glossopteris,* it was confined to the realm.

JURASSIC (200–140 m. yrs)

Global geography

Pangaea appears outwardly much as it did during the Permian and Triassic. But during the Jurassic we see the first incipient signs, particularly evident in southern Africa, of its fragmentation.

Global flora

Coniferous forests clothed the landscape of the Jurassic. Ginkgos, cycads, bennettitaleans and ferns were common.

Southern African strata

During the earlier part of the Jurassic desert sands accumulated in the desertic Gondwana interior. Then another of those devastating events which coloured earth's history began. Out of the crustal fissures marking the start of fragmentation, poured lava flow upon lava flow. This apparently continued unabated for some 50 million years, but with shifting focus as new rifts opened up around southern Africa. On a geological map of southern Africa, we see only scattered remnants of these lavas. There would originally have been a more or less continuous blanket over the whole region south of the Zambezi. Similar volcanic activity was widespread throughout the extent of the Gondwana Realm.

Southern African flora

The potential for unearthing plant remains in desert sands and sheet lavas is not great. A few foliage and silicified wood assemblages are known in Lesotho in oases in the upper desert sandstones (Cave Sandstones or Clarens Formation) and lower lavas (Drakensberg Lavas). Several localities in Lesotho have been sampled by French palaeobotanists, but the data is as yet unavailable. The collections are apparently dominated by conifers, with sphenophytes and bennettitaleans also present. The silicified wood also suggests conifers.

LOWER HALF OF CRETACEOUS (140–100 m. yrs)

Global geography

During the Cretaceous, continental drift is clearly seen to be in motion. Ever widening rifts have opened up between the southern continents.

Southern African strata

Seas flooded into the rifts demarcating southern Africa. Marine sediments are seen to occur on the continental shelf surrounding the whole region. This offshore sedimentation continued more or less uninterrupted throughout the Cretaceous.

Outside of the massive Congo Basin, with its riverine and lacustrine sediments, continental deposits were rare. In the earliest Cretaceous, onshore deposits (the Kirkwood Formation and equivalents) occur in the Algoa Basin behind Port Elizabeth; in scattered smaller basins situated in the valleys of the Cape fold belt; and down the eastern coastal plains of Natal and the Transkei.

Global flora

In the first half of the Cretaceous the character of plant life remained much like that of the Jurassic, with conifers still dominant and the cycads, ginkgos, bennettitaleans and ferns common. Quite suddenly (in geological terms), around the middle of the Cretaceous, something dramatic once again occurred. The gymnospermous plants were ousted by the angiosperms (flowering plants).

Southern African flora

The assemblages from the Kirkwood Formation and equivalents comprise a more or less typical Lower Cretaceous flora. In this case, the bennettitaleans make up the greater part of the collections, with conifers and a variety of ferns and fern-like plants being common. The total species tally is 28; around the same order found in the Permian Middle Ecca.

Well preserved spore and pollen assemblages occur throughout the sequence of offshore and onshore Cretaceous deposits.

POST LOWER CRETACEOUS (100 m. yrs to present)

Global geography

From the Middle Cretaceous onwards the southern continental plates have drifted steadily apart and generally northward; North America and Eurasia have likewise drifted apart; certain north-/south collisions, between Africa and Europe, and between India and Asia, have occurred.

Global flora

The angiosperms have become ever-more dominant and diverse globally, till now we have some 200 000 species of vascular plants on earth with some 20 000 species in South Africa.

Southern African strata

Exposed continental sediments representing this last 100 million year interval of earth history are seldom encountered in southern Africa. The sub-continent has experienced general uplift with the products of erosion being carried away by rivers to be deposited offshore on the continental shelf.

Southern African flora

The best megafloras are preserved in the open vents of Kimberlite pipes of various ages. The full development of the flora will be most successfully traced by the study of the innumerable spores and pollen grains preserved in the continuous pile of sediments on the continental shelf. Samples are readily available from the borehole cores resulting from the drilling activities of the oil companies.

Bothalia 14, 3 & 4: 345–354 (1983)

Intimations on the Tertiary vegetation of southern Africa

J. A. COETZEE*

ABSTRACT

Fossil pollen sequences from the Cape Peninsula and the Saldanha region indicate that sub tropical vegetation and climates existed in these regions during the Miocene. The pollen record from the Cape Peninsula may point to the extinction of some taxa by the terminal Miocene/Early Pliocene with the subsequent strong development of macchia. This major change can probably be related to the maximum build-up of the Antarctic ice-cap in the latest Miocene and the accompanying profound palaeoceanographic changes such as the major cooling of the Benguela current with its effect on the aridification of the Namib desert, and the global glacio-eustatic sea level drop.

Parallel palynological and lithological studies in the Saldanha region show that prominent Miocene vegetation shifts were linked to profound local changes in the palaeoenvironment associated with the northward migration of the Miocene Berg River. Such studies are of paramount importance for the possible assessment of the causes of changes in the palaeoenvironment and should first be carried out at many more sites over a wide region. It is to some extent premature to draw firm conclusions as to the origin and migration of some taxa in southern Africa. The record of very primitive angiosperms such as the *Clavatipollenites/Ascarina* complex and Winteraceae is of considerable phytogeographic interest.

RÉSUMÉ

INDICATIONS SUR LA VÉGÉTATION DU TERTIAIRE EN AFRIQUE AUSTRALE

Des séries de pollens fossiles de la Péninsule du Cap et de la région de Saldanha indiquent qu'une végétation et des climats tropicaux existaient dans ces régions durant le Miocéne. Le recensement des pollens de la Péninsule du Cap peut démontrer l'extinction de certains taxa à la fin du Miocène/début du Pliocène avec un fort développement du maquis. Ce changement majeur peut probablement être mis en rapport avec le développement maximum de la calotte glaciaire de l'Antarctique à la fin du Miocène et avec les profonds changements paléocéanographiques qui l'ont accompagné, tel que le refroidissement important du courant du Benguela donnant son aridité au désert du Namib, et la chute globale glacio-eustatique du niveau de la mer.

Des études palynologiques et lithologiques parallèles dans la région de Saldanha montrent que les changements de végétation remarquables du milieu du Miocène étaient liés aux profonds changements locaux dans le paleo-environnement associés avec la migration vers le nord de la Berg River du Miocène. De telles études sont d'une importance primordiale en vue d'une évaluation possible des causes de changements dans le paléo-environnement et devraient d'abord être conduites dans beaucoup d'autres sites dans une vaste region. Dans une certaine mesure, il est prématuré de tirer des conclusions fermes quant à l'origine et à la migration de certains taxa d'Afrique australe. Le recensement d'angiospermes très primitifs tels que le complexe Clavatipollenites/Ascarina *et les Winteraceae est d'un intérêt phytogéographique considérable.*

INTRODUCTION

The immense present day diversity of the biota of southern Africa, their phylogenetic relationships and adaptations to different environments are manifestations of important palaeogeographic events since the separation of Africa from Gondwanaland between Mid-Jurassic and Mid-Cretaceous times. During the rafting of this continent to its present situation it not only experienced the long-term development of the post-Gondwana physiographic features (Du Toit, 1966; King, 1967, 1978; Haughton, 1969; Truswell, 1970), but also the major Tertiary palaeoceanographic events of the Southern Ocean which profoundly effected global climates and biogeography. These were further greatly modified by the waxing and waning of the Pleistocene glaciations of the Quaternary, the degree of influence depending on the locality. In this connection a model has been synthesized for the Quaternary climates for southern Africa, based on a wealth of well-dated information (Van Zinderen Bakker, 1976; 1983). However, going further back in time to the Tertiary of southern Africa it becomes more difficult to reconstruct palaeoenvironments because of the lack of suitable fossil material or absolute dating. Palaeoecologies are also difficult to evaluate against the background of vastly different Tertiary climates compared to the present situation. Reconstructions of Tertiary vegetation on a palynological basis alone is not ideal but in recent years this discipline has become of immense significance in both the Northern and Southern Hemispheres. Although many palynomorphs of this period can be assigned to modern taxa (Muller, 1981), many of the microfloras of the rich and diverse assemblages may remain unidentified, often because of the extinction of the parent taxa. From a palaeoecological point of view difficulties also arise because some identifications can only be made to family level. Nevertheless the study of fossil pollen remains a very important source of information on past vegetation.

A recent synthesis on the Cretaceous and Tertiary vegetation history of southern Africa has been provided by Axelrod & Raven (1978) who have based their hypotheses on present phytogeographic distributions and a few inadequate fossil floras from Banke in Namaqualand (Kircheimer, 1932) and from the Knysna lignites (Thiergart *et al.* 1963).

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Recently, however, abundant microfossil evidence has become available from palynological investigations of a number of terrestrial deposits from different sites in the South-Western Cape which is now for the first time giving a picture of the Cainozoic vegetation and climatic history of at least the southernmost region of the subcontinent (Coetzee, 1978a, 1978b, 1980, 1981). They indicate the subtropical nature of the Tertiary vegetation of which some of the components, as in other Southern Hemisphere continents, have become extinct. The pollen sequences from the Langebaanweg area of the Saldanha region and from Noordhoek on the Atlantic coastline of the Cape Peninsula which have so far yielded the most interesting data, will form the basis of the present discussion (Fig. 1).

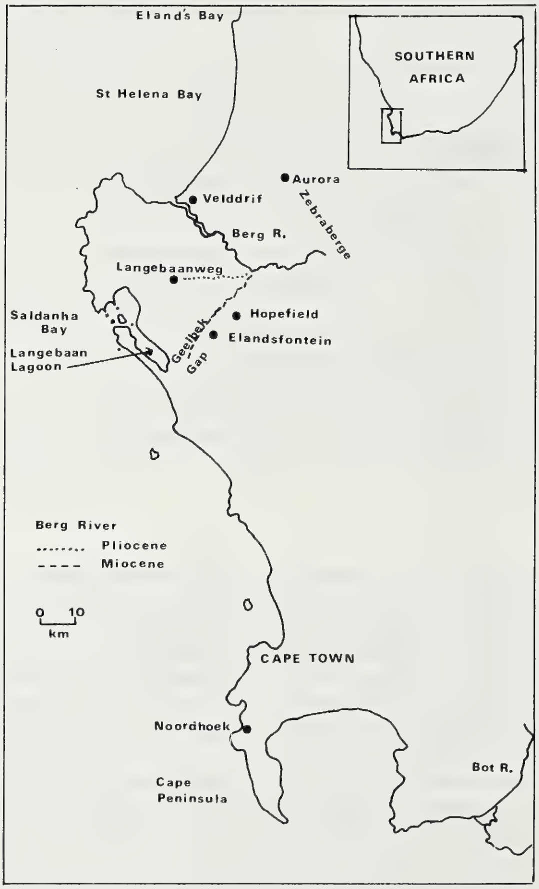

FIG. 1.—Locality map. From J. Rogers in Coetzee & Rogers (1982).

In recent years much attention is being paid to biogeographic patterns in the Southern Hemisphere. In this connection it is interesting that abundant micro- and macrofossil evidence from most of the Gondwana segments shows great similarities in their Tertiary Floras. This phenomenon and present day distribution patterns are, however, not easy to evaluate against the background of the present controversies on the methods and philosophies of biogeographic analysis. The vicariance school examines the vicariance of whole biotas as a result of continental drift and the subsequent postvicariance, as opposed to the fundamentally different view of long distance dispersal of individual components of biotas (Cracraft, 1980; McDowall, 1980). In this respect some of the palynomorphs from the Cape deposits which belong to the most primitive of angiosperms are of particular interest as the families to which they belong are extinct on this continent and have a disjunct distribution elsewhere.

PALAEOGEOGRAPHIC CONSIDERATIONS

Palaeoceanographic events

The well documented oceanographic events of the Tertiary in the Southern Ocean which have led up to the final glaciation of Antarctica have been of basic global biogeographical and palaeoenvironmental significance. This climatic evolution has been shown to be closely connected with plate tectonics, the far reaching effects of which have in recent years been described for the south-west Pacific by a number of authors such as Kemp (1978), Mildenhall (1980), Kennett (1980), Cracraft (1980), McDowall (1980), Coleman (1980) and others. From a biogeographical point of view as discussed for Australia (Kemp, 1978) it is also of great importance that the palaeolatitudes of the Gondwana segments and their concurrent positions in relation to the earth's pole of rotation have now been determined with some certainty from at least the Jurassic to the Late Miocene (Smith & Briden, 1977). Also of basic significance are the palaeotemperature curves for the Cainozoic estimated from oxygen isotope studies, for the bottom waters of the subantarctic (Shackleton & Kennett, 1975) and for the surface and bottom waters of the North Pacific (Savin, 1977 in: Frakes, 1979). Furthermore, the recent studies of global sea level cycles (Vail *et al.* 1977; Vail & Hardenbol, 1979) are receiving much attention in the explanation of palaeoenvironmental evidence.

As summarized by Kennett (1980), the main trend of Tertiary global climates is the general progressive climatic deterioration which was already initiated in the terminal Cretaceous. The underlying cause was the continuous breakdown of low latitude circulation and oceanic connections as a result of the progressive separation of the Gondwana segments until Antarctica finally became thermally isolated and situated across the pole. In this connection one of the most important events was the most precipitous drop (5°C) in temperature during the Cainozoic of the warm bottom ocean waters at the Eocene/Oligocene boundary (38 MY). This major change has been attributed to the progressive separation of Australia from Antarctica. Unrestricted flow of the Circum Antarctic Current set in after the final separation of these two continents by Mid- to Late Oligocene (30–25 MY) and the opening of the Drake Passage by 22 MY. It is significant that the largest relative fall in global sea level of the Cainozoic has been recorded for the Mid-Oligocene (30 MY) (Vail *et al.*, 1977; Vail & Hardenbol, 1979). It is also of importance that during this time the first weak spasmodic introduction of cold water into the Benguela Current has been recorded off the Walvis Ridge (Siesser, 1978).

The second profound climatic-glacial event was the development of the major ice-cap on East Antarctica and increased ice-rafting in the Middle Miocene (14–11 MY). It is significant in this regard that oceanographic studies off the Walvis Ridge indicate that the major cooling of the Benguela Current occurred in Late Miocene times with the subsequent rapid desiccation of the Namib Desert (Siesser, 1978). A marked increase in the ice volume of Antarctica occurred during the terminal Miocene (ca. 5 MY) which is estimated to have exceeded the present ice mass by about 50%. This was accompanied by a rapid northward migration of the Antarctic Convergence by 300 km and a marked global glacio-eustatic drop in sea level (200 m below the present sea level) (Vail *et al.*, 1977; Vail & Hardenbol, 1979; McKenzie *et al.*, 1979; Kennett, 1980). This important event which had far reaching biogeographical effects especially in coastal regions is considered to be partly responsible for the total isolation of the Mediterranean Basin and its salinity crisis (Messinian Stage) when it became tectonically closed off from the Atlantic inlet (McKenzie *et al.*, 1979). Evidence for this lowering of sea level has been recorded worldwide. These oceanographic changes have also been shown to be manifested in the cyclic transgressions and regressions of Miocene and Pliocene age in the southernmost parts of South Africa in the Saldanha region (Hendey, 1981a, 1981b; Coetzee & Rogers, 1982). These and other palaeogeographic events are basic to the explanation of the Tertiary biogeography of the south-western Cape.

Palaeotopography

Africa probably emerged from the Gondwana complex with segmented Gondwana biotas existing on a relatively flat Gondwana surface. Traces of the Great Escarpment of southern Africa were apparent at the close of the Karoo sedimentation in the Early or Mid-Jurassic and by Mid-Cretaceous it was already a prominent feature (King, 1967).

The subsequent evolution of the topographical features of the subcontinent has been described by King (1967, 1978) and it is important that by the end of the Tertiary 'the aspect of southern Africa was recognisably ancestral to the present' (King, 1978). Probably of particular interest with regard to the Tertiary vegetation of the Cape is the evolution of the Afromontane floristic Region (White, 1978; Axelrod & Raven, *l.c.*) along the eastern disjunct chain of mountains from Ethiopia along the Great eastern Escarpment to the southern Cape. From a phytogeographical point of view it is significant that the chain of high volcanoes in Ethiopia and East Africa are of early Miocene, Pliocene and Pleistocene age and could have afforded interrupted migration routes between the Northern and Southern Hemisphere during these periods (Axelrod & Raven, *l.c.*).

With regard to the south-western Cape, the topography is dominated by the Cape Folded Mountains of which the mountains of the Cape Peninsula are outliers. They are true orogenic mountains and are of Triassic age (Truswell, 1977). In Tertiary times they could have probably afforded some degree of altitudinal zonation or provincialism of vegetation especially in connection with the forests while the coastal lowlands probably harboured other ecosystems which must have been greatly influenced during the major Tertiary transgressions and regressions. The relationship between the geology and the present dominant macchia vegetation has been described by Lambrechts (1979).

PRESENT VEGETATION OF THE SOUTH-WESTERN CAPE

The present macchia (fynbos) vegetation in this area is unique and is one of the most interesting floras of the world. Because of its richness in species, the high degree of endemism (Goldblatt, 1978) and disjunct taxa, this floristic region, now known as Capensis (Werger, 1978; Taylor, 1978) has been regarded as one of six floral kingdoms of the earth. Many profound physical and climatic changes have contributed to the evolution of the remarkable diversity of this sclerophyllous vegetation in which restioid, ericoid and proteoid elements are characteristic. A detailed description of the vegetation including the marshes in the Saldanha region under discussion has been provided by Boucher & Jarman (1977).

Although it is considered to be a 'Mediterranean' flora, Capensis is distinct from other 'Mediterranean' floristic counterparts in many ways (Goldblatt, 1978). The area occupied by this floral Region has been variously delimited (Acocks, 1953; Levyns, 1964; Taylor, 1978; Goldblatt, 1978). Roughly it extends from the vicinity of Port Elizabeth, which receives all the year round precipitation, to the extreme south-western parts of the sub-continent where the climate at present is characterized by cyclonic winter rainfall and summer aridity under the influence of the Atlantic high pressure system and the cold upwelling of the Benguela Current. The interior of southern Africa receives summer rain and is dry in winter.

This vegetation is not confined to the south-western Cape, but has interesting outliers at increasing altitudes to the north in the mountains of the Karoo and Namaqualand and also in the north-east along the eastern disjunct chain of mountains of Africa as far as Ethiopia (Levyns, 1964; White, 1978; Killick, 1978). In agreement with Acocks (1953) and Goldblatt *(l.c.)* and contra Taylor *(l.c.)* and White *(l.c.)*, Capensis is here considered to include the temperate forest elements which survive in the Cape in moist ravines and sheltered niches. This forest flora is related to the mesophytic forests of the Afromontane Region (White, *l.c.)* and according to the present palynological record are certainly relics of the ancient Tertiary forests which covered this area millions of years ago (Coetzee, *l.c.)*. Also included in Capensis (Goldblatt, *l.c.*) in the drier valleys are elements of the Karoo Namib Region.

Recent accounts such as those of Axelrod & Raven *(l.c.)*; Goldblatt *(l.c.)* and Werger *(l.c.)* have given extensive reviews and discussions on the questions of the affinities, diversity, migrations and phytogeographical relationships of Capensis. The origin and age of this flora have been intriguing problems and conclusions have mostly been speculative. However, the recent palynological record indicates that the present vegetation of this floristic Region in the now mediterranean climate is of relatively recent origin and possibly owes its evolution primarily to the glacial history of Antarctica (Coetzee, 1978a, 1978b). The later vicissitudes of the Pleistocene epoch are probably responsible for the species richness and high degree of endemism (van Zinderen Bakker, 1976).

LITHOSTRATIGRAPHY AND AGE OF THE DEPOSITS

The only relative date for the palyniferous deposits at the sites under discussion is from the Langebaanweg area of the Saldanha region. Here the S1 borehole studied is south of the Varswater Quarry (Fig. 1), which is well known for its phosphate deposits and for the Early Pliocene Varswater Formation containing the richest fossil vertebrate assemblages of this age in Africa (Hendey, 1981a, 1981b). A definite age for the underlying Gravel Member of the 'Saldanha' Formation, also represented in the borehole, is not yet available at present although it had previously been assigned a Late Miocene age (Hendey, 1981). This latter Formation overlies the Elandsfontyn Formation which contains the palyniferous peat of the S1 borehole (Coetzee & Rogers, 1982; Hendey, 1981a). A firm age, for the Elandsfontyn Formation is, therefore, still problematical. The pollen assemblages of the peat including continous representation of Compositae, however, suggest a Late Miocene to Pliocene age range. In this connection it is interesting that *Aglaoreidia qualumis*, one of the pollen taxa present, has not been recorded as young as Late Miocene in Australia (A. Partridge, pers. comm.), where it was first described.

In the Noordhoek area the pollen sequences were analysed from the continuous S.20 core and parts of the O-core from boreholes drilled in a pocket of terrestrial sediments of Tertiary to Quaternary age (Fig. 1). At this site the palyniferous Elandsfontyn Formation is at present well below sea-level (−21 m to −50 m) (Rogers, 1980). Components of the rich and diverse pollen assemblages suggest an age younger than the Late Oligocene/Early Miocene boundary (Coetzee, 1978a) for this Formation at Noordhoek. Basic to this contention is the absence of Compositae pollen in the deepest levels and their rare occurrence in the upper levels of the cores from this Formation. In this connection, it is also significant that the pollen of the *Clavatipollenites*/*Ascarina* complex is abundant in the deeper levels of the Noordhoek deposits (−45 to − 32,4 m) and for the most part very rare in the upper levels (−32 to −20 m). In the Saldanha deposits no pollen of this group has so far been recorded. As some of the species of *Ascarina* are coastal plants, it is likely that they could also have existed at Saldanha and would have been recorded if the deposits were older.

Support for an age not older than the Late Oligocene/Early Miocene for the Noordhoek deposits comes from evidence of a major regression around southern Africa during the whole of the Oligocene and Early Miocene exposing much of the continental shelf to erosion (Siesser & Dingle, 1981).

TERTIARY VEGETATION AND PALAEOENVIRONMENTS

Vegetation (Figs 2 & 3)

The Tertiary microfossil floras from the two different areas contain taxa which are comparable to fossil palynomorphs of southern Hemisphere continents like Australia, Ninetyeast Ridge and New Zealand (Kemp, 1976, Kemp & Harris, 1977; Couper, 1960; Stover & Partridge, 1973; Mildenhall & Crosbie, 1979; Mildenhall, 1980). The Tertiary pollen assemblages from Noordhoek appear to indicate a continuous record from probably Early/Middle Miocene to the Pliocene while those from Saldanha represent some period in the Middle or Late Miocene. The tentative pollen zones (Coetzee, 1978a, 1978b) for the Noordhoek area are at present being refined and can therefore not yet be firmly correlated with those erected for Saldanha (Coetzee & Rogers, 1982). However, pollen evidence shows that in both areas, particularly at Noordhoek, mixed coniferous forests with tropical elements including several different palms, were more prominent during certain times while palms became dominant during other periods. During other intervals local swamp was more evident. At Noordhoek the pollen sequences show that some of these Tertiary elements became finally extinct and that other subtropical taxa no longer continued to exist there. The disappearance of this type of vegetation in this area probably occurred in the Pliocene as suggested by the time ranges of certain pollen taxa in other Southern Hemisphere continents and by comparison with pollen assemblages from Saldanha (Tankard & Rogers, 1978). It has also been shown that in this latter region woodlands and grasslands existed during the Early Pliocene which supported long necked giraffes, grazers such as alcelaphine antelopes, *Hipparion*, rhinoceros and the remarkable woodland bear, *Agriotherium africanum* (Hendey, 1980, 1981a).

During the forested periods of the Tertiary the following were among the forest pollen taxa recorded ('extinct' refers to Africa): *Podocarpus* spp. (Podocarpaceae); *Microcachryidites* sp. cf. *M. antarcticus* (Podocarpaceae, extinct); *Widdringtonia* (Cupressaceae); *Cupanieidites* sp. cf. *C. orthoteichus* (Sapidaceae, Cupanieae, tropical to subtropical); *Haloragacidites* sp. cf. *H. harrisii* (Casuarinaceae, extinct); Myricaceae; *Echiperiporites; Croton* sp. (Euphorbiaceae, tropical-subtropical); Palmae (subtropical to tropical, partly extinct); Myrtaceae; *Alchornea* sp. (*Psilatricolporites operculatus*, Euphorbiaceae, tropical); *Rauvolfia* sp. (*Margocolporites rauvolfii*, Apocynaceae, tropical); *Cunonia* sp. (Cunoniaceae); Sapotaceae, Combretaceae/Melastomataceae-type (subtropical-tropical); *Celtis*

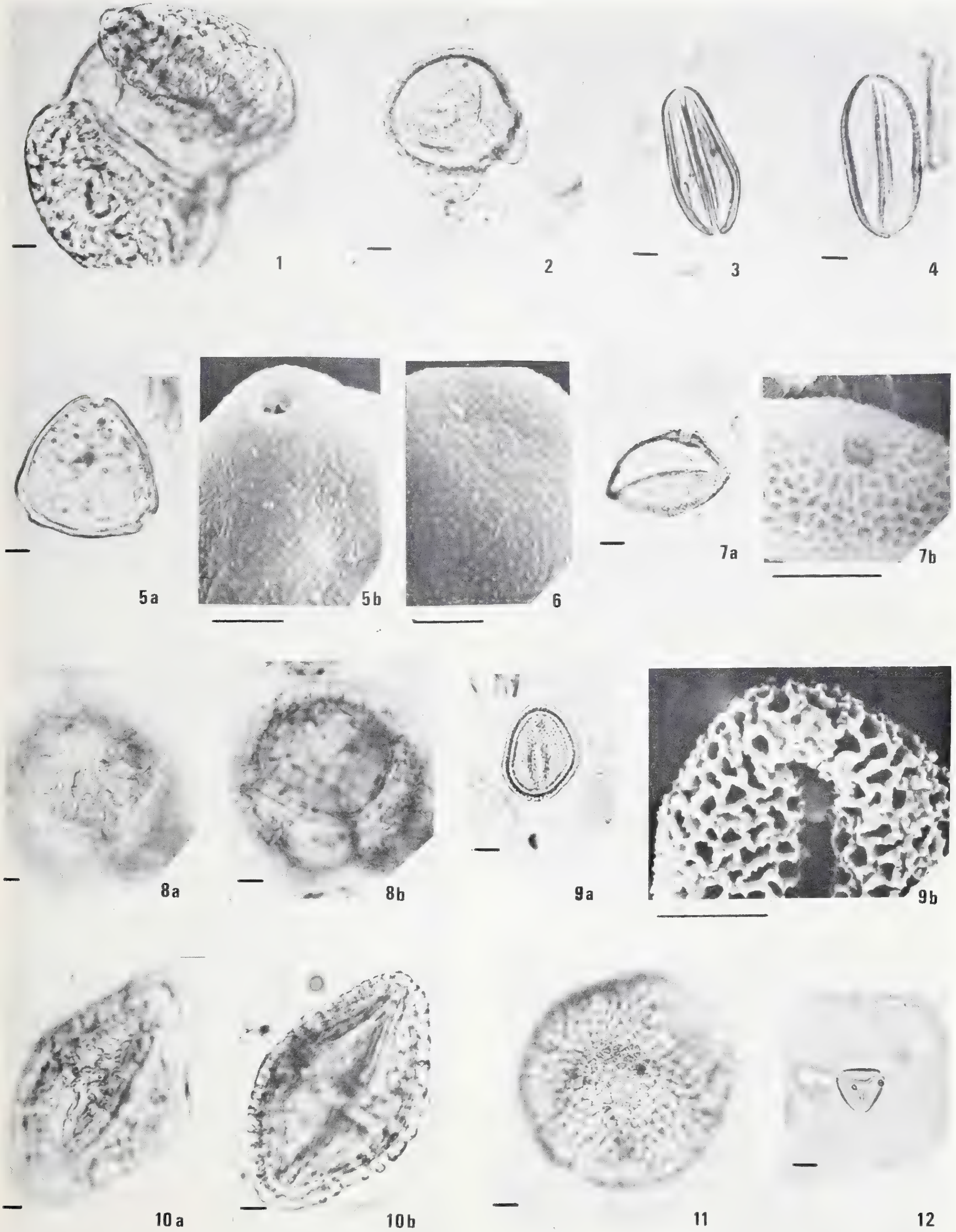

FIG. 2.—Fossil pollen of Miocene age from terrestrial deposits in the south-western Cape. Scale bars = 5 μm. Noordhoek: 1, Podocarpaceae; 2, *Microcachrydites* sp. cf. *M. antarcticus*; 3.4. Palmae; 5a, *Haloragacidites harrisii* (Casuarinaceae); 5b, scanning electron micrograph showing 'regularly spaced, minute grana borne on or at the intersections of vaguely defined linear elevations' (Kemp & Harris, 1977); 6, scanning electron micrograph of *Casuarina equisetifolia* (recent) revealing a similar surface configuration to 5b; 7a, *Aglaoreidia qualumis*, median focus showing annulus around the pore (see *A. qualumis* Partridge n. sp., Plate 20 figs. 8,9, (Stover & Partridge, 1973); 7b, scanning electron micrograph of the pore area; 8a, *Pseudowinterapollis* sp., tetrahedral tetrad, high focus showing the distal pore of a monad surrounded by the wavy reticulum; 8b, median focus showing clavate bacula; 9a, *Clavatipollenites*/*Ascarina* complex; 9b, scanning electron micrograph of colpus area; 10a, *Calodendrum* sp., high focus; 10b, median focus; 11, *Croton* sp., 12, *Cupanieidites* sp. cf. *C. orthoteichus*.

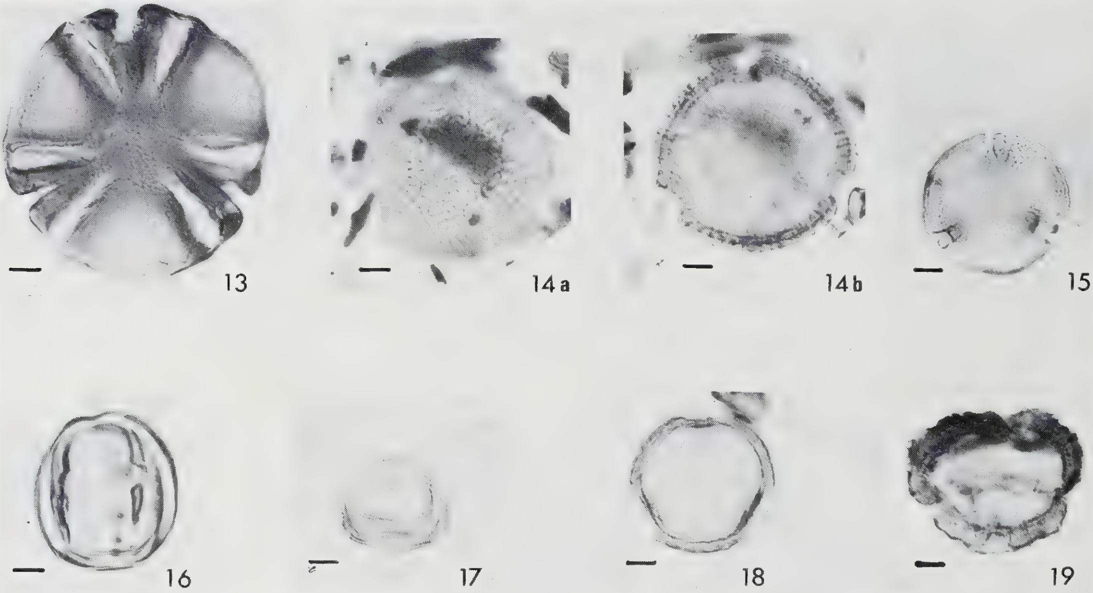

FIG 3.—Fossil pollen of Miocene age from terrestrial deposits in the south-western Cape. Scale bars = 5 μm. Saldanha & Noordhoek: 13, *Rauvolfia* sp. (*Margocolporites rauvolfii*) (Saldanha); 14a, *Canthium* sp. (Saldanha), high focus; 14b, median focus; 15, *Alchornea* sp. (*Psilatricolporites operculatus*) (Saldanha); 16, Combretaceae/Melastomataceae type (Noordhoek); 17, *Celtis* sp. (Saldanha); 18, *Cliffortia* sp. (Saldanha); 19, Compositae (Saldanha).

sp. (Ulmaceae); Taxa such as the *Clavatipollenites/Ascarina* complex (Chloranthaceae, extinct), *Pseudowinterapollis* (Winteraceae, extinct) and *Calodendrum* (Rutaceae) were only recorded at Noordhoek.

When the palms were dominant very few forest pollen taxa, of low diversity, were recorded and when marsh conditions were more evident the extinct *Aglaoreidia qualumis* Partridge, from Australia and Restionaceae were variously abundant. The affinity of the former taxon is not known but it is probably related to the Sparganiaceae.

With regard to the evidence of macchia vegetation during the Tertiary in these areas, pollen data indicate that some elements like the Proteaceae and Restionaceae were consistently present and variously abundant. In the Noordhoek area, Thymelaeaceae, Gramineae and Ericaceae were extremely sparsely recorded from a time before the first appearance of the Compositae, whereas *Cliffortia* and *Stoebe* (Compositae) appeared sporadically at respective later stages. In the Saldanha area these macchia elements, without Ericaceae, were already established in the Miocene period studied (but with low percentages of pollen and contained more Gramineae).

Palaeoenvironments

In an attempt to reconstruct the local Tertiary palaeoenvironments in connection with the above vegetation changes along these coastal areas, it is considered to be of paramount importance to carry out parallel detailed lithological and palynological studies. So far in the case of the Saldanha area this has been achieved with very interesting results (Coetzee & Rogers, 1982). The pollen zones here indicate a retrogressive succession from a mixed tropical coniferous forest containing palms to palm dominated vegetation and finally to a local swamp with abundant *Aglaoreidia qualumis* and Restionaceae.

These vegetational changes are consistent with the lithological details from the Elandsfontyn Formation at the S1 site and the wider Saldanha-Hopefield region which indicate a fluctuating fluviatile environment associated with a meandering Miocene Berg River (Rogers, 1980, 1982). In this case the tropical forest was probably riparian. As the river changed its course this gallery forest probably gave way to a dominant palm situation as drainage deteriorated (Moore, 1973) on a proximal developed floodplain. Further flooding, as a result of the S1 site becoming a distal floodplain, probably caused the deterioration of the palm vegetation and the development of a fresh water swamp (Coetzee & Rogers, 1982). The Berg River which is the most important river in the south-western Cape has gradually migrated from its palaeovalley south of the Langebaan Lagoon (Rogers, 1980), to a Pliocene estuary near the S1 site (Hendey, 1981a) to its Quaternary position on the shore of St Helena Bay (Fig. 1).

PHYTOGEOGRAPHICAL CONSIDERATIONS

Theories of the phytogeographical distribution of the flora of Capensis have suggested that the taxa of this floristic Region have arrived there from different Southern Hemisphere sources in ancient times, whereas others originated relatively recently from tropical African elements. (Levyns, 1964;

Goldblatt, 1978; Johnson & Briggs, 1975; Axelrod & Raven, 1978). With the present knowledge of continental drift, palaeolatitudes of continents and the extensive palynological evidence now available from all the Southern Hemisphere continents, it may be possible to shed some light on these problems although much more evidence and multidisciplinary research from more localities are required.

The wide distribution of similar Tertiary floras especially in the southern Hemisphere is significant in connection with the vegetation of this period in southern Africa as this continent was the first to leave Gondwanaland, although direct austral biological links between Africa and Australasia existed via South America until Senonian times (Jardine *et al.*, 1974). It has been suggested (Levyns, 1964; Axelrod & Raven, 1978; Goldblatt, 1978) that some taxa reached Africa by long distance dispersal across a narrower Indian Ocean from Australasia via Ninetyeast Ridge (emergent in the Palaeocene) and the Mascarene Plateau including India, in the early Tertiary. In the Palaeocene Southern Africa with its long history as an island continent was, however, already situated at 15° further south than now, and India, according to the Palaeocene map of Smith & Briden (1977), was well separated from the southern continents. According to Leroy (1978), direct migrations between India-Madagascar and Australia had already become more difficult by Mid-Cretaceous times [Madagascar separated from Africa about Mid-Cretaceous (ibid)].

The phytogeographical aspects of some of the most significant pollen taxa of the Tertiary flora now extinct in the south-western Cape such as Palmae, Casuarinaceae, *Clavatipollenites* sp. and *Pseudowinterapollis* sp. have already been alluded to (Coetzee, 1978a, 1981). With more data available some of these taxa will be further digressed on in the following discussion.

As a consequence of its former position in the Gondwana complex, the early vegetation that covered these southern lands must to some extent have been shared by southern Africa although some provincialism of vegetation must have existed over the huge former land mass. Until at least Eocene times southern Africa situated at 50°S, like Southern Australia (Smith & Briden, 1977), must have experienced the high humidity and warmth of the early Palaeogene climate (Kemp, 1978; Frakes, 1979). This kind of climate could have maintained floras in southern Africa that were similar to those of the other Gondwana segments.

Ancient Angiosperms

It is of particular interest that pollen of the most ancient of Angiosperms, the *Clavatipollenites/Ascarina* complex and *Pseudwinterapollis* sp., another primitive angiosperm has been documented in the Noordhoek deposits (Coetzee, 1981).

(a) *Clavatipollenites/Ascarina* complex. The most recent discussion on the distribution, range and taxonomy of this palynomorph has been provided by Muller (1981). The microfossil *Clavatipollenites hughesii* Couper, first described from the Barremian of England, has been considered to belong to the most ancient of angiosperms. In the Southern Hemisphere it has mainly been referred to as *Clavatipollenites* sp. cf. *C. hughesii* (Kemp & Harris, 1977). A strong affinity, however, exists between this pollen type and that of *Ascarina* (Chloranthaceae) which ranges from the Upper Cretaceous to the present in New Zealand (Mildenhall, 1980). This similarity has been the subject of continuous debate and in his consideration of the problem Muller (1981) agrees with Kemp & Harris (1977) to 'restrict the record for *Ascarina* to the Tertiary and indicate the possible identity of *Clavatipollenites hughesii* as Chloranthaceous with the oldest record as Aptian and to indicate it as *Ascarina* type'. According to the available records and ranges, Muller *(l.c.)* has demonstrated the continuity between *Clavatipollenites* sensu stricto and *Ascarina* and concludes that the Chloranthaceae or the ancestral group dates back to the Aptian and was dominant in the lower Cretaceous. Indications are that they were coastal plants.

The most restricted ranges for this pollen type are recorded in Brazil and Central Africa where the plants were eliminated in the Middle Cretaceous as a result of a drier climate (Muller, *l.c.).* In this connection it is significant that this microfossil, also recorded in off-shore sediments of Lower Cretaceous age (younger than Barremian) along the eastern and southern South African coasts (Scott, 1976; MacLachlan & Pieterse, 1978), is abundantly recorded in the Tertiary deposits at Noordhoek. It became extinct here, probably in the Late Miocene, before the last of the tropical Tertiary components of the vegetation disappeared. It was not recorded in the S1 borehole at Saldanha.

The Chloranthaceae do not occur in Africa today and the four genera have a very disjunct present distribution in the tropics. In this connection the presence of *Ascarina* today in Madagascar is an interesting phytogeographical phenomenon (Coetzee, 1981; Straka, 1966).

(b) *Pseudowinterapollis* (Winteraceae) is another interesting pollen taxon recovered from the Noordhoek deposits which probably became extinct in the Late Miocene/Early Pliocene (Coetzee, 1981). This family does not occur in Africa today but is confined to South America and the South Pacific and one species, *Takhtajania perrieri* occurs in Madagascar. This microfossil type, also recorded from the Upper Cretaceous and Tertiary of Australia and New Zealand (Stover & Partidge, 1973; Mildenhall & Crosbie, 1979; Mildenhall, 1980), is similar to the pollen of the extant *Drimys* (South America and Pacific). The only known fossil record of the Winteraceae from the Northern Hemisphere are the fossil leaves of *Drimys* from the upper Eocene from Oregon (Praglowski, 1979). This record from the south-western Cape adds to the knowledge of the wider past distribution of this family.

The ancient forest

The Cretaceous and Palaeogene rain forests of most of the Southern Hemisphere continents show a number of interesting similarities and give indications that Temperate Podocarp-Auracarean coniferous forests with *Nothofagus* spp. were mixed with tropical rain forest taxa (Cranwell, 1964; Kemp, 1978; Mildenhall, 1980). With regard to the important components of these forests it is, however, interesting that *Auracaria* that was still present in the Upper Cretaceous in the south-western Cape (McLachlan & Pieterse, 1978) probably became extinct before the beginning of the Palaeocene. It occurs, however, in the Palaeogene of India (Lakhanpal, 1970). *Nothofagus*, on the other hand has so far not been recorded in either the Cretaceous or Tertiary of southern Africa and is absent from deposits of this age in India and from Ninetyeast Ridge. This genus which seems to have had an Upper Cretaceous origin (Mildenhall, 1980) had probably not evolved by the time Africa and Greater India separated from Gondwanaland.

The Casuarinaceae, another Southern Hemisphere family, to which the form-genus *Haloragacidites harrisii* Couper has been assigned was an important constituent in the Tertiary forests of most of the Gondwana segments. The presence of this taxon in India has not been confirmed. This family does not occur in Africa today, but fossil pollen of this genus has been recorded at Noordhoek. Unconfirmed similar fossil pollen types have been recorded from Banke and the Knysna lignites. The possibility that this dispersed pollen belongs to the Casuarinaceae has already been discussed (Coetzee, 1978a). In this connection it is significant, as in other above mentioned cases, that *Casuarina equisetifolia* is indigenous to Madagascar (Straka, 1976). In Australia the Casuarinaceae were tropical components of the early rain forests and the megafossil records show that they belonged to the Division Gymnostomae which were the only type occurring before the separation of Australia from Antarctica. The fossil record from Patagonia supports a Gondwana distribution for these taxa. Casuarinaceae of the sclerophyllous Cryptostomae Division developed in Australia only after the separation of the two continents in the Eocene and during the progressive deterioration of the climate while the Gymnostomae became depleted (Christophel, 1980). It is possible that the microfossils assigned to the Casuarinaceae in southern Africa may have come from parent taxa of the Gymnostomae occurring in rainforests and that they became extinct in the south-western Cape at the end of the Miocene also perhaps as a result of the deterioration of the climate and progressive aridity. Macrofossil evidence, however would have to provide this information as the pollen from the two Divisions is difficult to distinguish.

Johnson & Briggs (1975) suggest that the Proteaceae of Australia and southernmost Africa originated in the Australian section of Gondwanaland in mixed mesothermic forests which became segmented with the separation of the complex. The first reliable microfossil evidence dates from Maestrichtian (Muller, 1981). Earlier occurrences are not yet certain (Dettman, 1981). According to Johnson & Briggs *(l.c.)* this family is probably derived from mesothermic tree forms and could have arrived together with the gymnosperms, Podocarpaceae, *Widdringtonia* and other forest elements in Southern Africa. In this connection it is significant that *Proteacidites* has been recorded in the Cenomanian to Maestrichtian of the off-shore sediments in the south-western Cape (McLachlan & Pieterse, 1978). It must be pointed out, however, that *Proteacidites* does not necessarily include Proteaceae. Among the interesting components of these forests in southern Africa were probably Monimiaceae, fossil wood of which has been recorded from the Late Cretaceous of Pondoland, eastern Cape Province (Axelrod & Raven, 1978). The extant monotypic genus *Xymalos*, still occurring in these regions is also found today in Madagascar. Also recorded at Noordhoek is *Cupanieidites* sp. cf. *C. orthoteichus* a member of the Sapindaceae (Cupanieae) with a Gondwana distribution. The first occurrence of the Cupanieae dates from the Coniacian in the Late Cretaceous of Africa and India (Muller, 1981). *Calodendrum* of the primitive Diosmeae (Rutaceae) was also present among these Tertiary taxa at Noordhoek.

Macchia (Fynbos) elements

The Proteaceae and Restionaceae, [the latter also regarded by Johnson & Briggs (1981) as an old southern family] are well represented in the pollen assemblages of the Tertiary in the south-western Cape. These authors suggest that the evolution and diversification of ancestral sub-families of the Proteaceae had already taken place in the pre-Australian section of Gondwanaland. Comparison of the diversities of the early Tertiary form-genera of the south-western Cape and Australia remains to be evaluated. The Restionaceae, also of pre-Australian Gondwana origin, are first recorded from the Palaeocene and are considered to show a single ancient phytogeographic link with Africa (Johnson & Briggs, *l.c.)*. It is also of interest that this family has a widespread Tertiary record in both hemispheres (Ladd, 1977).

Other Fynbos microfossil elements such as those belonging to the Compositae [with a late Tertiary appearance of *Stoebe*-type, Thymelaeaceae, *Cliffortia*, Graminae and Ericaceae (the latter not recorded at Saldanha)] were very sparsely represented until probably the Pliocene (as shown at Noordhoek) when the first strong development of Fynbos is evident from the pollen assemblages. By this time all traces of tropical Tertiary forest elements including the palms had disappeared (Coetzee, 1978a, 1978b). It has been suggested (Coetzee, *l.c.)* that this profound vegetation change is linked to the palaeoceanographic events associated with the maximum build-up of the Antarctic ice-sheet in the Terminal Miocene. However, according to Johnson & Briggs (1981) the present sclerophyllos communities of south-western Australia and the south-western Cape are rather the result of the progressive development of nutrient deficient soils than of the evolution of a mediterranean climate. They consider that these conditions already started in the Palaeogene in forests where nutrient deficiency at certain sites gave rise repeatedly to scleromorphic forms. This change could have been associated with the deterioration of the climate, but under rainfall conditions permitting summer growth. The growth rhythm of the present Fynbos suggests an origin in summer rainfall conditions (Taylor, 1978). It is significant that at present macchia does not spread onto high nutrient soils in the mediterranean climates of either the Cape or Australia (Johnson & Briggs, *l.c.).*

It is not certain when the mediterranean type of climate set in in the south-western Cape as a consequence of the maximum Antarctic glaciation. Palaeontological evidence from the Saldanha area suggests that the transition from a probable monsoon climate to a mediterranean climate could have been in the early Pliocene. Precipitation must have been decreasing but a summer-wet/winter-dry climate was probably still prevailing. (Hendey, 1981b).

CONCLUDING REMARKS

Palynological evidence has indicated the existence of sub-tropical Tertiary vegetation in the south-western Cape from a period probably later than the early Miocene to possibly the early Pliocene. Many of the pollen taxa are similar to the Tertiary form-genera of other Southern Hemisphere continents. The continuous pollen sequence for this period from the Cape Peninsula suggests that most components of this type of vegetation had become eliminated by the early Pliocene. These extinctions and the dominant development of Fynbos vegetation are probably primarily related to major palaeoceanographic and palaeoenvironmental changes associated with the glacial evolution of Antarctica. In this connection the major cooling of the Benguela current and the aridification of the present Namib desert in the Late Oligocene must have initiated profound effects on the vegetation which continued into the Pliocene. According to Tankard & Rogers (1978) the progressive aridity of the subcontinent dates from the latter epoch. The pronounced sea level regression recorded on the South African continental shelf near the Miocene/Pliocene boundary (Siesser & Dingle, 1981) may have enhanced coastal dry conditions. Hendey (1981a) has correlated this event with the global glacio-eustatic sea level drop at 6,6–5,2 MY (Vail & Hardenbol, 1979). It is possible that these dry conditions could have affected extinctions of taxa like the *Clavatipollenites/Ascarina* complex.

It has, on the other hand, also been suggested that, as in south-western Australia, the dominant expansion of macchia in the Cape was due to the existence of nutrient deficient soils rather than to the change to a mediterranean climate. They consider this type of climate to have been superimposed on already pre-adapted scleromorphs. With regard to the origin and migration of the macchia vegetation much more palynological and lithological studies are essential before firm conclusions can be made.

The interpretation of local Tertiary shifts in vegetation as demonstrated by parallel lithological and palynological studies in the Saldanha region stresses the need for such detailed investigations at many more cites over a wide area before general conclusions on regional vegetation changes during this epoch can be made. In the Saldanha region a monsoon climate (Hendey, 1981b) may have been responsible for the palaeoenvironmental changes. The possible high humidity of this period may be related to the global climatic optimum of the Miocene between 17 and 15,5 MY (Haq, 1980), the global high sea level of the Middle Miocene (Vail & Hardenbol, 1979) and the transgression of 16 MY along the S.W. African coast (Hendey, 1981b). A warm ocean and still warmer epicontinental seas could have contributed to the high humidity.

Many of the Tertiary vegetation elements including conifers, Palmae, Proteaceae, Restionaceae, the *Clavatipollenites/Ascarina* complex, Winteraceae and cf. Casuarinaceae could be of direct austral origin. The occurrence of these groups in the Tertiary of the south-western Cape and the disjunct distribution of some of these taxa in Madagascar could pose interesting problems in connection with vicariance and post vicariance biogeography.

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Evolution des flores et de la végétation Tertiaires en Afrique, au nord de l'Equateur

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RÉSUMÉ

La répartition de la flore Tertiaire en Afrique, très différente de l'actuelle, se comprend si on tient compte de deux facteurs essentiels: la régression des mers épicontinentales vers le nord et la dérive du continent africain. Il en résulte qu'à l'Eocène inférieur, l'équateur se trouvait à environ 1 000 km au nord de sa position actuelle. Ces modifications aboutissent à des transformations importantes de l'environnement climatique et par conséquent de la répartition des flores.

Cela explique notamment la présence d'une mangrove en Libye avec *Sonneratioxylon aubrevillei* et en Egypte avec *Nipa burtinii.*

La forêt dense est présente dans le Paléocène du Tinrhert avec *Entandrophragmoxylon normandii* (comparable à l'actuel *Entandrophragma angolense*). Les formations de forêt dense, développées à l'Eocène, surtout sur le rivage, sont suivies plus au sud, d'une savane qui s'étend davantage à l'Oligocène et qui peut atteindre la mer.

Cependant, on trouve encore en bordure de mer à l'Oligocène, des espèces de forêt dense comme *Entandrophragmoxylon magnieri* (comparable à *Entandrophragma candollei*) espèce qui avoisine des dépôts deltaiques avec de grands troncs qui indiquent une flore plus sèche (*Detarioxylon aegyptiacum, Combretoxylon bussonii* et *Pterocarpoxylon tibestiense* (rapproché du *Pterocarpus erinaceus* de savane), mais parfois accompagnée de troncs de forêt-galerie (*Atherospermoxylon aegyptiacum,* Monimiacée).

Au Miocène, l'assèchement continue et la savane progresse. Les Palmiers apparaissent et des galeries forestières subsistent, mais même à proximité de la mer, le biotope est sec au Miocène inférieur dans le Nord de l'Afrique. Ce n'est que vers le sud que la végétation hygrophile apparait au niveau du Tibesti avec *Myristicoxylon vincentii.*

Ainsi, près de la position présente de l'Equateur, la mangrove se retrouve au Sénégal dans le Paléogène du Cap-Vert avec des pollens de Rhizophoracées, Sonneratiacées, *Avicennia* et *Nipa (Spinizonocolpites)* et la forêt dense subsiste dans sa position actuelle entourée d'une savane.

ABSTRACT

EVOLUTION OF THE TERTIARY FLORA AND VEGETATION IN AFRICA NORTH OF THE EQUATOR

The distribution of the Tertiary flora in Africa is very different from the present one, if one takes into account two main factors: the regression of the epicontinental seas towards the north and the drifting of the African continent. From this it appears that in the lower Eocene, the Equator was about 1 000 km further north than its present position. The modifications resulted in important changes in the climatic environment and therefore the distribution of the floras.

This explains, for instance, the existence of a mangrove in Libya with Sonneratioxylon aubrevillei *as well as* Nipa burtinii *in Egypt.*

The dense forest is present in the Paleocene of Tinrhert with Entandrophragmoxylon normandii *(similar to the present* Entandrophragma angolense). *The dense forest formations, developed in the Eocene, mainly on the banks, are followed, more in the south by a savanna expanding further in the Oligocene and able to reach the sea.*

However, one still finds on the coast in the Oligocene, dense forest species such as Entandrophragmoxylon magnieri *(similar to* Entandrophragma candollei) *species neighbouring the delta deposits with tall trunks, indicating a drier flora:* Detarioxylon aegyptiacum, Combretoxylon bussonii *and* Pterocarpoxylon tibestiense *(close to* Pterocarpus erinaceus *of the savanna, but sometimes accompanying trunks of the gallery-forest* (Atherospermoxylon aegyptiacum, *Monimiaceae).*

In the Miocene, the drying process continues and the savanna progresses. Palm trees appear and the gallery-forests remain, but only in the vicinity of the sea, the biotope is dry in the lower Miocene in north Africa. It is only towards the south that hygrophilous vegetation appears at the level of Tibesti with Myristicoxylon vincentii.

So, near the present position of the Equator, the mangrove is found in Senegal in the Paleogene of Cape Verde with some pollen of Rhizophoraceae, Sonneratiaceae, Avicennia *and* Nipa (Spinizonocolpites) *and the dense forest in its present position, surrounded by the savanna.*

GÉNÉRALITÉS

Au Tertiaire, la végétation africaine avait une répartition tout autre qu'actuellement. Sa reconstitution est fondée sur des fossiles très différents: bois, empreintes de feuilles, graines, fruits, spores et pollens. Or, la classification botanique est basée sur la fleur. Déterminer un pollen, une feuille ou un bois revient à dire comment est constituée la fleur.

Les bois fossiles ne peuvent être déterminés que par comparaison avec les bois actuels. Pour les bois tertiaires d'Afrique, l'identité de certains plans ligneux fossiles et contemporains laisse supposer que les fleurs étaient, sinon identiques, tout au moins très peu différentes.

Les difficultés de détermination tiennent à de nombreuses causes: 1, les plans ligneux actuels ne sont pas tous connus; 2, des espèces fossiles peuvent ne plus être représentées dans la flore actuelle; 3, les

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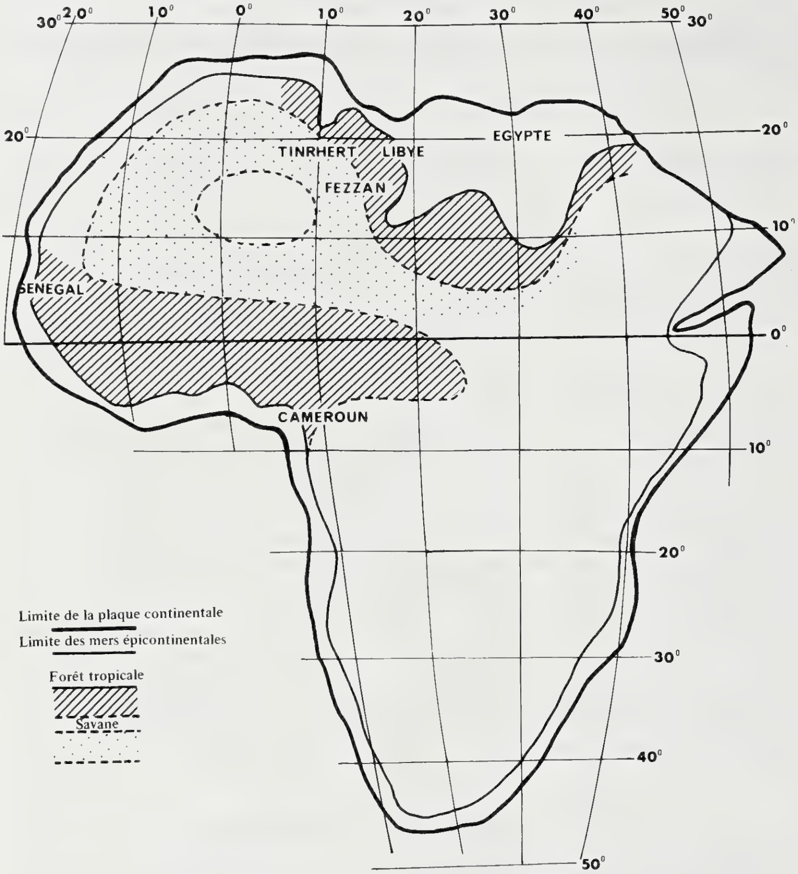

Fig. 1.—Répartition des flores au Nord en Afrique à l'Eocène inférieur, il y a 50 millions d'années. Remarquer la position de l'Equateur avec sa forêt dense et la présence d'une forêt de type tropical au Nord en bordure de mer. La savane unit les deux ensembles.

plans ligneux peuvent présenter des variations au cours de l'ontogénèse, et suivant la place occupée dans l'arbre (jeunes rameaux, racines) par rapport au bois adulte stabilisé; 4, certains fossiles ayant des caractères très répandus et, par conséquent peu significatifs, ne peuvent être déterminés avec précision; 5, la fossilisation a pu détruire des caractères importants (ponctuations, septes, cristaux). Rares sont les cas favorables où des caractères saillants permettent d'arriver au genre, exceptionnellement à l'espèce.

Quant à l'âge géologique précis, il est souvent difficile à établir sauf si le fossile a été trouvé 'en place' dans les sédiments. Les bois récoltés en surface peuvent provenir d'une couche de terrain plus récente dont les sédiments encaissants ont disparu; les bois fossiles abondants en de nombreux points de l'Afrique posent ce problème essentiel. Les troncs souvent très grands que l'on rencontre se sont-ils fossilisés sur place ou ont-ils été l'objet d'un transport avant la minéralisation? De nombreuses hypothèses ont été émises qui portent précisément sur le mode de minéralisation de ces fossiles.

On a estimé avec raison que les bois égyptiens s'étaient déplacés avec les eaux d'un fleuve se jetant dans la vallée du Nil en les déposant dans un vaste delta situé à 200 km au sud du Caire et s'étendant d'est en ouest sur 600 km. Une silicification sur place doit bien, semble-t-il, être rejetée; dans de nombreux cas, il y a d'abord charriage, comme le prouve la gangue de certains bois enrobés dans un poudingue de cailloux roulés. Cette constatation, bien établie pour l'Egypte, est valable en de nombreux points du Sahara, où pareillement la répartition présente des fossiles est le résultat d'un transport qui explique en particulier certains groupements où le flottage des bois a pu mélanger des espèces de savane et des formes de forêt dense.

Les transports d'espèces végétales peuvent affecter les spores et les pollens, faussant pareillement les répartitions et leur interprétation. Le vent est souvent considéré comme étant à l'origine des déplacements, surtout dans le cas des formes anémochores. Les animaux jouent un rôle appréciable. Le transport jusqu'au point de fossilisation est avant tout hydrodynamique. Le pollen est léger et sa production abondante. A la suite d'une dispersion inégale, il en résulte un aéroplancton qui se sédimente principalement en suspension aqueuse sur une aire continentale (lacs, rivières, mares et par voie fluviatile) ou dans les alentours marins.

On peut apporter un autre élément d'explication aux déplacements des zones de végétation en Afrique en faisant appel à la dérive des continents.

FLORES TERTIAIRES

L'étude de la flore du Nord de l'Afrique au Tertiaire doit tenir compte du fait qu'à la fin du

Crétacé, les mers épicontinentales recouvraient une grande partie du Continent formé de grandes îles parmi lesquelles la région du Hoggar en constituait une importante. Cette flore tertiaire comptait essentiellement des Angiospermes possédant des bois hétéroxylés, s'opposant ainsi à la flore de l'époque secondaire du Continental intercalaire, caractérisée par les espèces ligneuses homoxylées, bien qu'un certain nombre d'Angiospermes y avaient déjà été signalées, notamment à Dibella (Niger).

Sahara occidental (Rio de Oro)

Néogène

Le Mio-Pliocène de la région de Villa-Cisneros a livré: *Detarioxylon aegyptiacum* Boureau & Louvet (1973)*, *Caesalpinioxylon (Berlinioxylon) quirogae* (Schenk), *Sapindoxylon almelai* Koeniguer (Sapindaceae); *Bombacoxylon (Dombeyoxylon) owenii* (Carr.) Gottwald (1969)** et *Pinuxylon pineoides* Kraus (Koeniguer, 1967). Il s'agit d'une flore plutôt sèche.

Maroc

Paléogène

Les phosphates yprésiens de Khouribga ont livré un *Pterocarpoxylon arambourgii* Boureau (1951), comparable aux plans ligneux de l'actuel *Pterocarpus santalinioides* qui est un petit arbre du bord des rivières et des lagunes, de *P. mildbraedii*, grand arbre des forêts denses semi-décidues en Côte d'Ivoire, ainsi que de *P. pedatus* d'Indochine qui est également un arbre de grande taille.

Une flore éocène a été signalée dans la vallée de l'Ouest M'goun dans le sud du Maroc par Depape & Gauthier (1952) avec des formes incertaines rappelant *Rhizocaulon* et *Diospyros*.

Algérie

Paléogène

(a) Au Paléocène, dans le Tinghert oriental, on a décrit une Méliacée fossile, *Entandrophragmoxylon normandii* Louvet qui rappelle l'actuel *Entandrophragma angolense* de la forêt dense ainsi que des Légumineuses d'écologie non précisée comme *Leguminoxylon zemletense, L. tamendjeltense, L. monodii* et *L. medarbaense* Louvet (1968).

(b) Au-dessus des derniers calcaires hamadiens, près de Fort-Flatters, dans le Continental terminal, on a décrit avec un âge éocène moyen à Oligocène:

— des Légumineuses: *Leguminoxylon menchikoffii* Boureau (1951) dont le plan ligneux rappelle celui d'espèces actuelles de la forêt dense ombrophile d'Afrique tropicale *(Calpocalyx, Erythrophleum, Kaoue, Xylia, Pentaclethra, Afzelia), Leguminoxylon bonnetti* Boureau & Koeniguer (1967), *L. schenkii* Koeniguer, *L. submenchikoffii* Boureau & Koeniguer, *Detarioxylon aegyptiacum* Boureau & Louvet, *Afzelioxylon kilianii* louvet (1965);

— des Méliacées: *Lovoaxylon princeps* Louvet (1966), voisin de *Lovoa trichilioides* des forêts humides où il accompagne *Entandrophragmoxylon normandii* Louvet (1968);

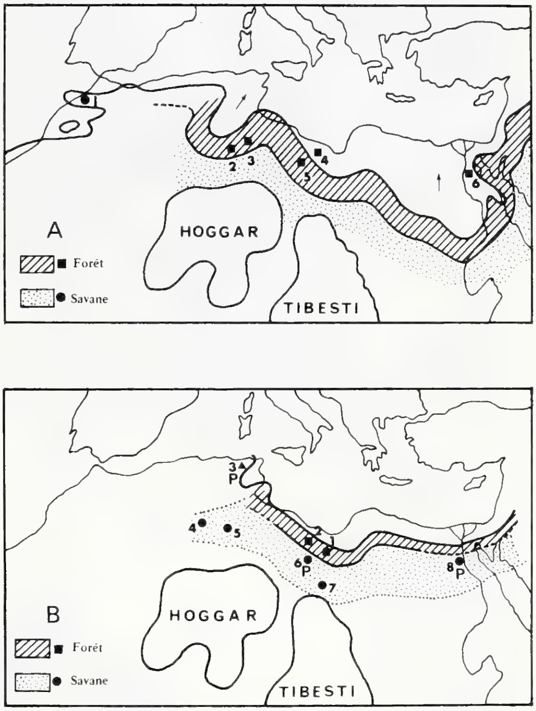

FIG. 2.—Cartes synthétiques montrant les déplacements probables de la forêt dense et de la savane à l'Eocène et à L'Oligocène dans le Nord de l'Afrique, Hachures obliques: forêt dense; pointillés: savane. A. Trait appuyé: rivages marins à l'Eocène inférieur et moyen. 1, *Pterocarpoxylon arambourgii* (Yprésien); 2, *Entandrophragmoxylon normandii* (Eocène); 3, *Lovoaxylon princeps* (Eocène); 4, *Sonneratioxylon aubrevillei* (Lutétien supérieur); 5, *?Flacourtioxylon gifaense* (Lutétien supérieur); 6, *Nipadites sickenbergeri* (Lutétien). B, Trait appuyé: limite méridionale des mers à l'Oligocène moyen et supérieur. 1, *Entandrophragmoxylon magnieri* (Oligocène). 2, *?Ficoxylon melahense* (Oligocène); *Bombacoxylon (Dombeyoxylon) owenii* (Oligocène); 4, *Detarioxylon aegyptiacum* (Oligocène probable); 5, *Combretoxylon bussonii* (Oligocène inférieur); 6, *Combretoxylon bussonii* (Oligocène); 7, *Combretoxylon bussonii, Detariophyllum coquinense, Pterocarpophyllum erinacoides* (Oligocène); 8, *Combretoxylon bussonii, Detarioxylon libycum* (Oligocène); P, *Palaeomastodontinés* (Oligocène). Le trait séparant la forêt dense de la savane représente en réalité une limite très perméable aux formations sèches qui peuvent gagner la mer.

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* *Nicolia aegyptiaca* Unger (1859) est une espèce qui a subi de nombreuses vicissitudes dans sa synonymie:
= *Sterculioxylon aegyptiacum* (Unger, 1859) Kräusel (1939);
= *Detarioxylon libycum* Boureau & Louvet (1970);
= *Detarioxylon aegyptiacum* (Unger 1859) Boureau & Louvet (1973).
On trouve ce plan ligneux dans tout le Tertiaire et le Quaternaire avec une vaste répartition en Afrique: Rio de Oro, Libye, Fezzan, Egypte, Afrique orientale. Il se rapproche de l'actuel *Detarium microcarpum* des flores sèches des régions, 'soudano-guinéennes' selon l'appellation de P. Louvet.

** *Dombeyoxylon owenii* (Carr.) Kräusel (1939), du Tertiaire égyptien est devenu *Bombacoxylon (Dombeyoxylon) owenii* (Carr.) Gottwald (1969). Il se rapproche de *Rhodognaphalon stolzii* (Ulbr.) Robyns (1963) (syn. *Bombax stolzii* Ulbr.), espèce de forêt sèche de l'Est africain qui a probablement la même écologie.

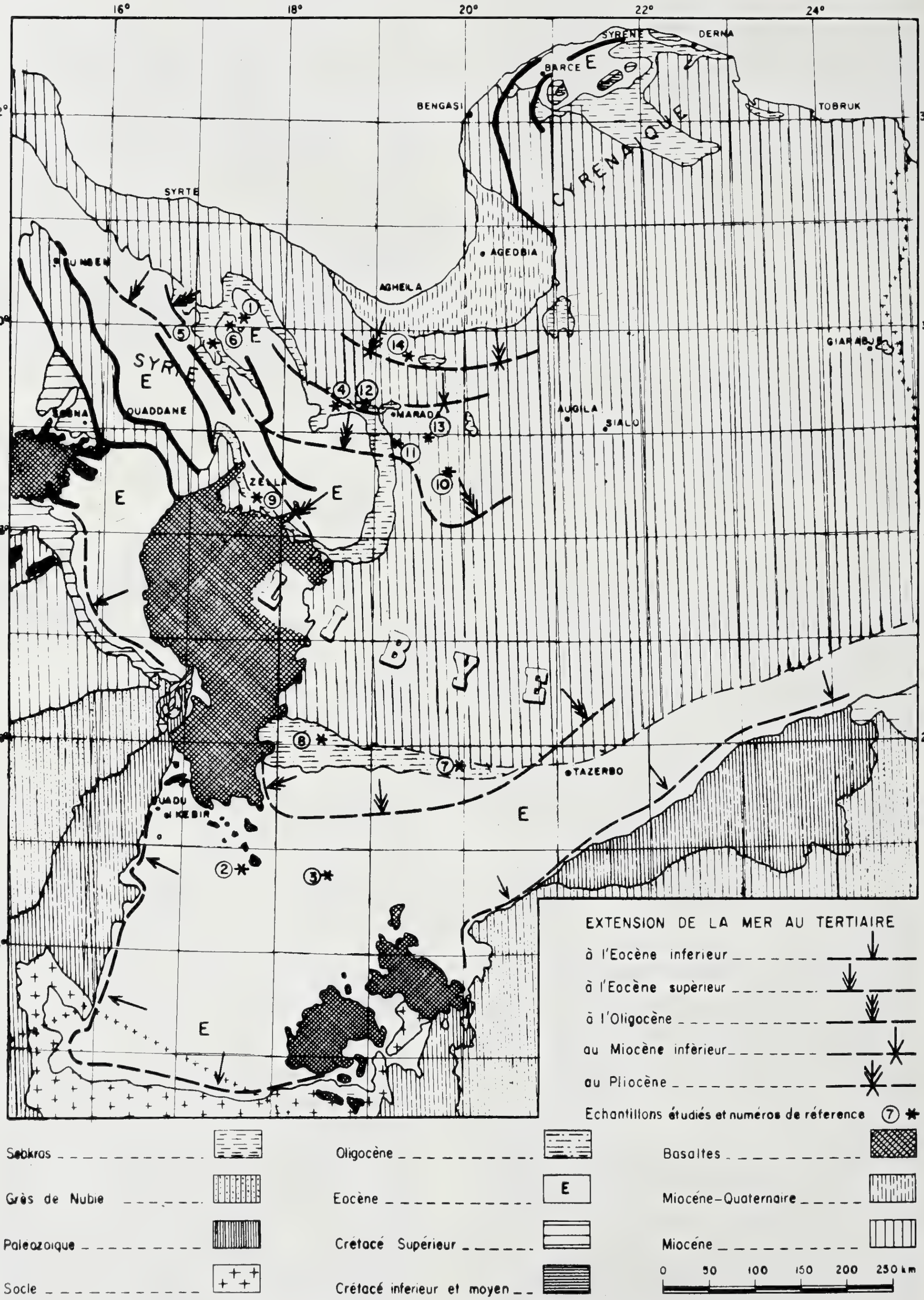

FIG. 3.—Rivages successifs de la mer au Tertiaire en Libye. Références des gisements (d'après P. M. Magnier, 1971). 1, Graret Abd el Fadel (Lutétien supérieur); Ouest de Ouaou en Namous (Eocène inférieur ou moyen); 3, 100 km Est de Ouaou en Namous (Paléocène ou Eocène inf.); 4, Gara Gehannem, formation Greir bu Hascisc (Oligocène); 5, Dor el Melah, formation Greir bu Hascisc (Oligocène); 6, Dor el Abd (Oligocène); 7, Djebel Coquin Est (Oligocène); 8, Djebel Coquin Ouest (Oligocène); 9, Zella el Ghetia (Oligocène); 10, Djebel Zelten Sud, faciès 'Zelten' (Miocène inférieur); 11, Gara el Cra, faciès 'Zelten' (Miocène inférieur); 12, Gara Gehannem, faciès 'Zelten' (Miocène inférieur); 13, Gur el Menghil, faciès 'Marada-Zelten' (Miocène inférieur); 14, Sahabi (Mio-Pliocène).

— des Combretacées: *Combretoxylon (Anogeissuxylon) bussonii** Louvet (1973) voisin de l'actuel *Anogeissus leiocarpus* de la savane;

— des Euphorbiacées: *Euphorbioxylon lefrancii* Boureau (1951), voisin des *Anthostema* d'Afrique tropicale et de Madagascar;

— des Guttifères: *Guttiferoxylon barryi* Delteil-Desneux (1967);

— des Palmiers: *Palmoxylon aschersonii* Schenk.

(c) L'Eo-oligocène d'In Salah a livré *Harunganoxylon vismioides* Fessler-Vrolant & Starostin (1979), Hypéricacée qui indique probablement une galerie forestière.

Néogène

La région de Tindouf (Dalaat el Admia, Algérie), d'âge vraisemblablement oligo-miocène a fourni: *Rubioxylon (Mitragynoxylon) gevini* Koeniguer & Lemoigne, 1971, retrouvé dans le centre du Sud-Tademait, de même que *Dombeyoxylon (Bombacoxylon) owenii* (Carr.) Gottwald (1969), *Quercoxylon gevinii* Boureau (1949) et *Leguminoxylon menchikoffii* Boureau (1951). La vallée du Chelif a livré un Palmier daté de façon incertaine: *Palmoxylon aschersonii* Schenk, rappelant *Borassus aethiopum,* retrouvé en Algérie orientale à Tebessa (Boureau, 1947).

Le Miocène inférieur du Douar Mogada a donné *Caesalpinioxylon mogadaense* Boureau (1950), voisin des actuels *Berlinia* et *Macrolobium* de Côte d'Ivoire. L'Atlas algérien a donné *Scytopetaloxylon sp., Cynometroxylon* sp. et *Sapindoxylon (Blighioxylon) koholense* Koeniguer (Néogène?).

Tunisie

Paléogène

Oligocène. Une liste de Fliche (1888) signale dans l'Oued Mamoura: *Bambusites thomasii* Fliche, *Palmoxylon cossonii* Fliche (voisin de l'actuel *Borassus aethiopum* et à Aïn Cherichira: *Araucarioxylon aegyptiacum* Kraus, *Ficoxylon cretaceum* Schenk (décrit par Fessler-Vrolant, 1979), *Acacioxylon antiquum* Schenk, *Ebenoxylon (= Jordania) ebenoides, E. tenuetanum;* un *Bombacoxylon owenii* (Carr.) Gottwald (1969) et un *Pseudolachnostyloxylon weylandii* Gottwald (1969), proviennent de l'Oligocène d'El Aroussa. *Ficoxylon guettarense* Fessler-Vrolant (1976) est oligocène dans le Nord tunisien. L'Oligocène supérieur du Djebel Ech Cheid a donné *Terminalioxylon tunesense* Duperon-Laudoueneix (1973), *Copaiferoxylon copaiferoides* Fessler-Vrolant (1977) (voisin de l'actuel *Copaifera* de forêt dense) associé à un *Tetrapleuroxylon* sp. aff. *T. acaciae* (Krausel) Muller-Stoll et Mädel (Delteil-Desneux & Fessler-Vrolant, 1976). Ces formes sont associées à *Terminalioxylon cheidense* Fessler-Vrolant (1980). Il s'agit en fait d'un mélange de formations claires et de forêts-galeries dans un Djebel de la Tunisie du Nord, en bordure de mer.

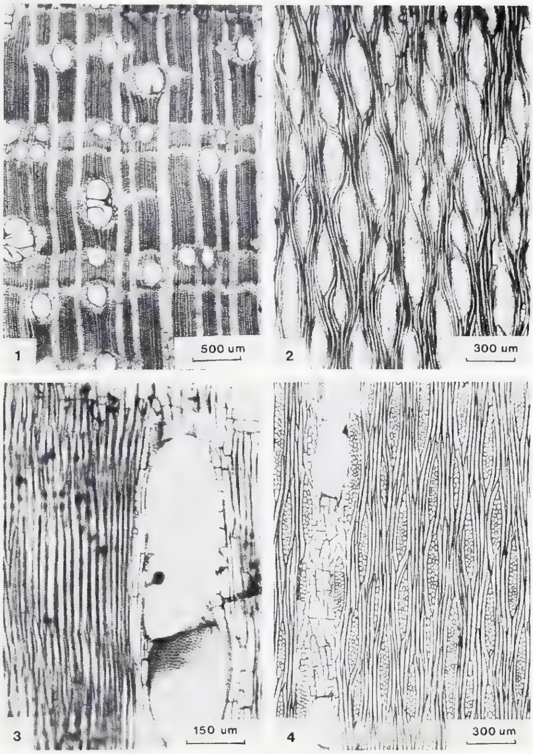

FIG. 4.—*Detarium microcarpum* Gill. et Perr. Coll. GTFT 6604. Guinée. Espèce actuelle. Savane. 1, coupe transversale montrant les pores diffus, le parenchyme circumvasculaire aliforme, le parenchyme circummédullaire, deux rangées de canaux sécréteurs verticaux et les files de fibres alternant avec des files plus étroites correspondant aux extrêmités brusquement effilées des fibres; 2, coupe tangentielle montrant les rayons homogènes souvent disséqués par l'élongation des fibres; 3, coupe radiale montrant une perforation simple et les ponctuations intervasculaires alternes, moyennes à grandes. Les fibres étagées ont des extrêmités brusquement effilées et imbriquées. Présence de files de cellules cristallifères. *Detarium macrocarpum* Harms. Coll. CTFT 5475. Espèce actuelle. Forêt dense; 4, coupe tangentielle montrant les rayons ayant souvent 2—3 cellules terminales dressées. Les dissections des rayons par l'élongation des fibres sont moins fréquentes et moins prononcées que chez *D. microcarpum.*

Néogène

(a) *Miocène.* Miocène inférieur, Djebel Nara: *Terminalioxylon tunense, Cynometroxylon tunense, Swartzioxylon naraense* (Delteil-Desneux). Miocène moyen: Myricaceae, *Carya,* Méditerranée, Europe (Planderova, 1971).

(b) *Pliocène.* Une flore de la fin du Pliocène collectée sur la rive nord du lac Ichkeul (Arambourg, Arênes & Depape, 1951), révèle des affinités relevant du domaine tropical (*Salix canariensis, Cassia, Sapindus, Pittosporum*) alors que d'autres appartiennent au domaine boréal, voire même eurosibérien *(Salix alba, Fagus silvatica, Ulmus scabra).* Sivak (1977) y rencontre des pollens de *Cathaya* et de *Tsuga,* et Delteil-Desneux (1979) signale un *Euphorbioxylon sapindoides* qu'elle

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* *Combretoxylon bussonii* Louvet (1973), s'est appelé antérieurement *Anogeissuxylon bussonii* Louvet (1964), Combretacée très proche de l'actuel *Anogeissus leiocarpus* à répartition africaine assez vaste: Haute-Guinée, Sénégal, Gambie, région du Nil, Abyssinie et région préforestière de la Haute Côte d'Ivoire. C'est un témoin des forêts sèches de transition soudano-guinéenne succédant à la forêt dense tropicale.

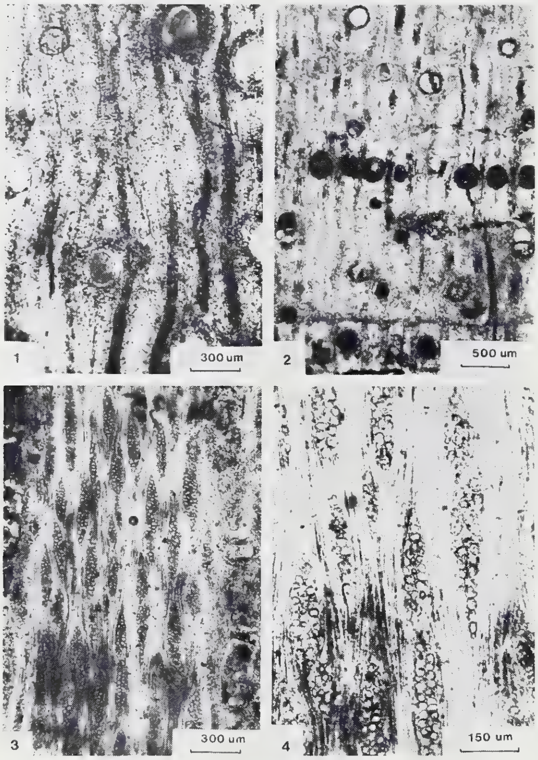

FIG. 5.—*Detarioxylon aegyptiacum* Louvet & Boureau (1970). Holotype. Coll. *Boureau* 1514 B, CFP PF 548B. Eocène probable de la région de Ouaou en Namous (Libye). 1, coupe transversale montrant la disposition diffuse des pores, le parenchyme circumvasculaire à tendance aliforme et les rangées de fibres à diamètre normal alternant avec des rangées à diamètre plus faible correspondant aux extrêmités brusquement effilées des fibres; 2, autre coupe transversale montrant le parenchyme circummédullaire et une bande de canaux sécréteurs verticaux; 3, coupe tangentielle montrant la disposition des rayons homogènes souvent disséqués par l'élongation des fibres; 4, autre coupe tangentielle à un plus fort grossissement.

rapproche des actuels *Anthostema,* petits arbres des galeries forestières et des lisières de forêts marécageuses.

L'étude des spores et pollens du Bassin néogène de Monastir atteste un climat tropical avec un paysage de mangrove ou d'arrière-mangrove. A côté de cette basse contrée humide et marécageuse, certains reliefs portent des végétaux plus ou moins xérophiles (Demarcq *et al.*, 1976).

Libye

Paléogène

L'Eocène et l'Oligocène de la Syrte offrent des affleurements bien datés. L'intrication des faciès marins et continentaux suggère un flottage de faible importance et une proximité probable des biotopes d'origine et des emplacements de sédimentations. Les fossiles sont datés du Lutétien au Pliocène par les faunes marines dans les faciès correspondant à des bordures de mer où les débris végétaux ont été entraînés sur des restes de vertébrés dont plusieurs gisements sont datés sans ambiguïté. Dans ce dernier cas, les restes végétaux ont été récoltés en place et de véritables forêts d'arbres fossilisés ont permis la découverte des feuilles correspondantes dans les mêmes séries gréseuses. Ce bassin tertiaire montre une régression régulière, vers le nord, de la mer située à la place de la Méditerranée.

(a) *Eocène.* En bordure de mer, le Lutétien supérieur a livré *Sonneratioxylon aubrevillei* Louvet (1970), espèce rappelant les actuels *Sonneratia apetala* et *S. acida* de la mangrove. Un gisement (30° Nord et 16°48'Est) a donné *Flacourtioxylon gifaense* Louvet (1970), qui est probablement une Rhizophoracée (Louvet, 1972). Ces bois sont situés immédiatement au-dessus du niveau à *Nummulites gizehensis* du Lutétien supérieur. Rappelons que *Nipa burtinii,* dont l'écologie est comparable, est associé à *Nummulites gizehensis* en Egypte.

D'après Ph. Magnier qui a collecté ces bois, les rivages éocènes libyens avec leurs fossiles et leurs récifs rappellent ceux des régions tropicales de l'Océan Indien et de l'Australie du Nord où des formations denses succèdent à la mangrove et passent à des formations plus sèches dans les régions continentales. Dans la région d'Ouaou en Namous

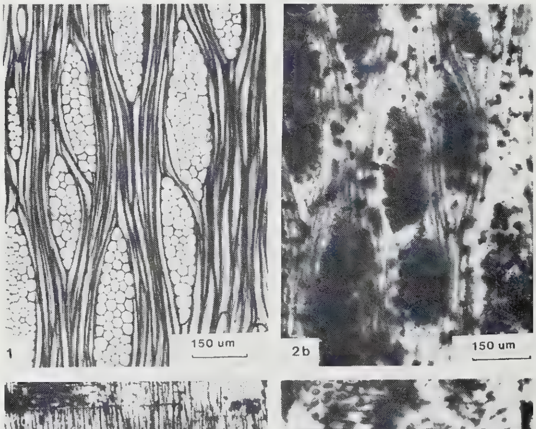

FIG. 6.—1. *Detarium microcarpum* Gill. et Perr. Coll. *CTFT* 6604. Guinée. Espèce actuelle. Coupe tangentielle montrant les rayons homogènes disséqués par l'élongation des fibres. 2, *Detarioxylon aegyptiacum* Louvet & Boureau (1970). Holotype. Coll. Boureau et Lefranc 5443. Eo-oligocène du Tinrhert*. a, coupe tangentielle, comparable à la précédente, montrant des rayons homogènes identiques disséqués par l'élongation des fibres; b, coupe radiale montrant l'étagement des fibres, les files de cellules cristallifères, les cellules couchées et les cellules terminales carrées des rayons; c, ponctuations intervasculaires aréolées, alternes, petites à grandes, paraissant ornées.

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* Les échantillons de ce gisement ont été décrits en 1969 sous le nom de *Sterculioxylon aegyptiacum* (Unger) Kräusel.

du Fezzan (Eocène inférieur probable), on a trouvé *Combretoxylon bussonii, Detarioxylon aegyptiacum, Pterocarpoxylon tibestiense* Louvet & Boureau (rapproché de l'actuel *Pterocarpus erinaceus* de savane). *Sterculioxylon freulonii* Boureau (1957), est voisin de l'actuel *Sterculia elegantiflora.* Alors que la présence d'une mangrove doublée d'une forêt dense humide est très probable en bordure de la côte, les échantillons d'Ouaou en Namous caractérisent une flore plus sèche, mais son implantation ne peut être précisée car certains bois ont pu être flottés. Les couches de passage de l'Eocène à l'Oligocène ont donné un fruit bien défini, le *Fezzania calanchoensis* Boureau (1956), dans le Fezzan. Il s'agit d'une Apocynacée (ou Asclepiadacée).

(b) *Oligocène.* En bordure de mer, on a trouvé *Entandrophragmoxylon magnieri* Louvet (1974), rapproché de l'actuel *Entandrophragma candollei,* c'est-à-dire une Méliacée de forêt dense. Ce bois devait vivre près d'une lagune littorale où survivaient les dernières *Nummulites* et où il a été transporté. L'Oligocène de Dor El Abd (Syrte) a livré *Bridelioxylon arnouldii* Koeniguer (1966), Euphorbiacée voisine des *Bridelia,* de la forêt dense et de la savane.

Dans les gisements continentaux, à l'est du Djebel Coquin, on a décrit *Combretoxylon bussonii* Louvet.

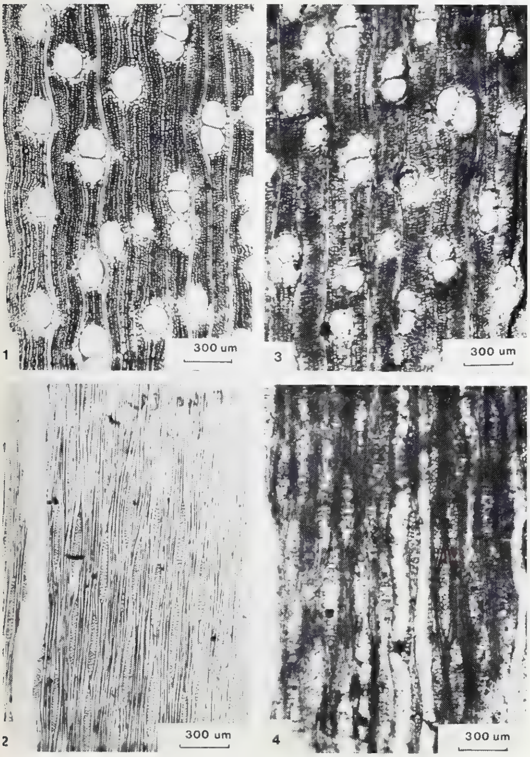

FIG. 7.—1 et 2, *Lovoa trichilioides* Harms (Dibétou). Espèce actuelle. Coll. *CTFT* 2140. 3 et 4, *Lovoaxylon princeps* Louvet (1966). Coll. *Boureau* 3103, *Busson* 1140. Eo-oligocène du Tinrhert; 1 et 3, coupes transversales montrant la disposition diffuse des vaisseaux, le parenchyme circumvasculaire entourant incomplètement les vaisseaux et quelques cellules de parenchyme dispersé; 2 et 4, coupes tangentielles montrant les rayons homogènes surtout 3–4 sériés.

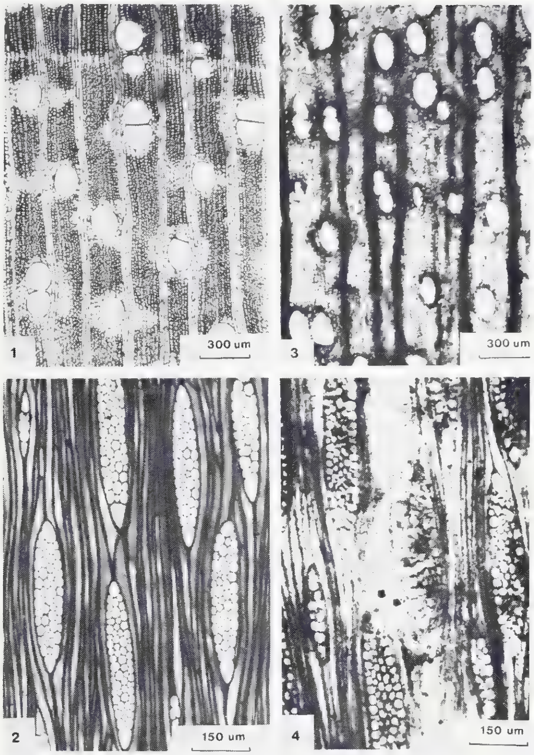

FIG. 8.—1–2, *Entandrophragma angolense* C.DC. (Tiama). Coll. *CTFT* 14953. Côte d'Ivoire. Espèce actuelle. 3–4, *Entandrophragmoxylon normandii* Louvet (1968). Holotype. Coll. *Boureau* 5216, *Busson* 5446A. Eo-oligocène du Tinrhert. 1 et 3, coupes transversales montrant le parenchyme circumvasculaire à tendance aliforme et une bande de parenchyme circummédullaire; 2 et 4, coupes tangentielles montrant les rayons à tendance homogène et leur cellule terminale dressée.

D'autre part, à l'ouest du Djebel Coquin, on a décrit des empreintes de feuilles: *Naucleaphyllum* Louvet & Mouton (Rubiacée) *Caesalpinites erythrophleoides* Louvet & Mouton, *Detariophyllum coquinense* L. & M. rappelant l'actuel *Detarium microcarpum* de savane (Césalpiniacées), *Milletiaphyllum obtusum* L. & M. *Erythrinaphyllum parvisenegalense* L. & M., *Pterocarpophyllum erinacoides* L. & M., rappelant l'actuel *Pterocarpus erinaceus,* de savane (Papilionacées).

A Zella, à moins de 100 km du rivage marin présumé, on a trouvé *Combretoxylon primigenium* Louvet (1973), Combrétacée de savane associée à *Palaeomastodon intermedium.* Des formations denses paraissent avoir subsisté en bordure de mer alors que dans les régions continentales domine un biotope sec en pleine expansion susceptible d'atteindre localement la mer.

Néogène

Le Miopliocène est dans l'ensemble caractérisé par une flore plus sèche avec de nombreux Palmiers. Les bois hétéroxylés des gisements de Sahabi El Giofa montrent des zones semi-poreuses nettes, indiquant un climat à saisons contrastées sèches prononcé.

Miocène inférieur. Les gisements situés à proximité de la mer, ont livré:

- *Xymaloxylon (Monimiaxylon) zeltenense* Louvet (1974), Monimiacée
- *Palmoxylon aschersonii* Schenk
- *Caesalpinioxylon craense* Louvet. Cesalpiniacée
- De nombreux *Combretoxylon (Anogeissuxylon) bussonii* Louvet et de *Bombacoxylon (Dombeyoxylon) owenii* Gottwald
- *Pahudioxylon gehannemense* Louvet. Cesalpiniacée
- *Pterocarpoxylon syrtense* Louvet. Papilionacée

Bombacoxylon owenii, des mêmes gisements que *Combretoxylon bussonii* et *Detarioxylon aegyptiacum* Louvet & Boureau, indique une flore sèche. *Palmoxylon aschersonii,* rapproché de *Borassus aethiopum,* palmier de savane souvent présent dans des galeries forestières, permettrait d'expliquer son association avec *Xymaloxylon zeltenense,* les Monimiacées vivant actuellement dans les lieux humides des forêts denses de moyenne et haute altitude. *Pahudioxylon gehannemense* présente des affinités avec *Afzelia africana,* espèce plus sèche pouvant pénétrer dans des formations plus denses. Cet ensemble indique un biotope sec à proximité de la mer du Miocène inférieur.

Plus au sud, au Tibesti, *Myristicoxylon vincentii* Koeniguer, peut être Miocène, pourrait traduire une végétation forestière relativement hygrophile, appartenant sans doute à la bande forestière équatoriale.

Au Miocène supérieur (Tortonien-Messinien), à proximité de la mer en Libye, dans une flore probablement sèche, on a signalé *Leguminoxylon sahabiense* Louvet (1976), voisin des actuels *Acacia* et *Dichrostachys,* et accompagné d'un *Palmoxylon* sp. aff. *P. libycum* (Stenzel) Kräusel, Palmier voisin des *Phoenix,* à rapprocher d'une espèce connue dans l'Oligocène supérieur et le Miocène de la Basse-Egypte et de la Syrte (Kräusel & Chiarugi) et retrouvé par Koeniguer (1969) en Libye dans le Mio-Pliocène.

Egypte et Soudan

Paléogène

(a) Le Danien-Montien de Kosseir, près de la Mer Rouge, a donné des fruits et des graines: *Anonaspermum aegyptiacum* Chandler (1954), dont la désignation se rapproche de celle des feuilles du Crétacé d'Assouan *(Anona assouaniana,* Fritel) et de divers bois tertiaires du Sahara soudanais [*Annonoxylon striatum,* Boureau (1950), et *Annonoxylon edengense* Boureau (1954)]. Ces couches intermédiaires ont également livré des Euphorbiacées (*Lagenoidea trilocularis* et *L. bilocularis* Reid & Chandler (1933). Le genre est connu depuis 1933

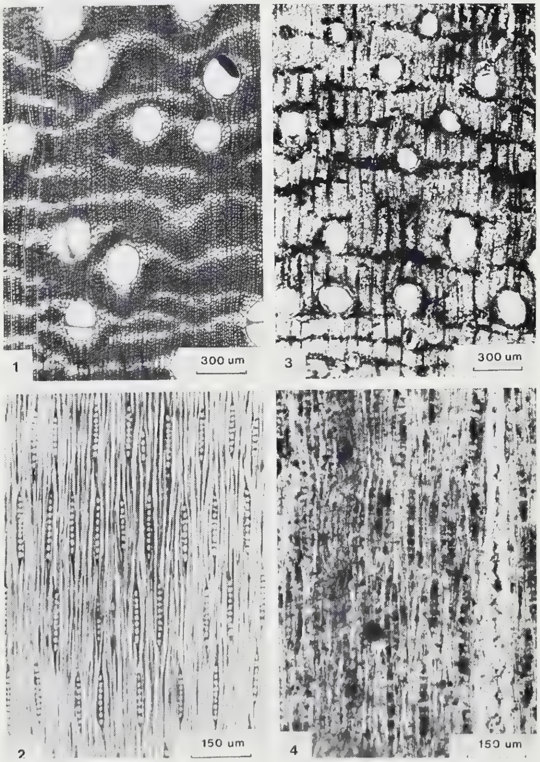

FIG. 9.—1 et 2, *Pterocarpus erinaceus* Poir. Coll. *CTFT* 6906 Sénégal. Espèce actuelle. 3 et 4, *Pterocarpoxylon tibestiense* Louvet & Boureau 1970. Coll. *Boureau* 1514A, *CFP* PF 548A. Eocène de la région de Ouaou en Namous; 1 et 3, coupes transversales montrant la disposition des vaisseaux et le parenchyme circumvasculaire très aliforme formant des bandes tangentielles plus ou moins continues; 2 et 4, coupes tangentielles montrant l'étagement des rayons unisériés homogènes.

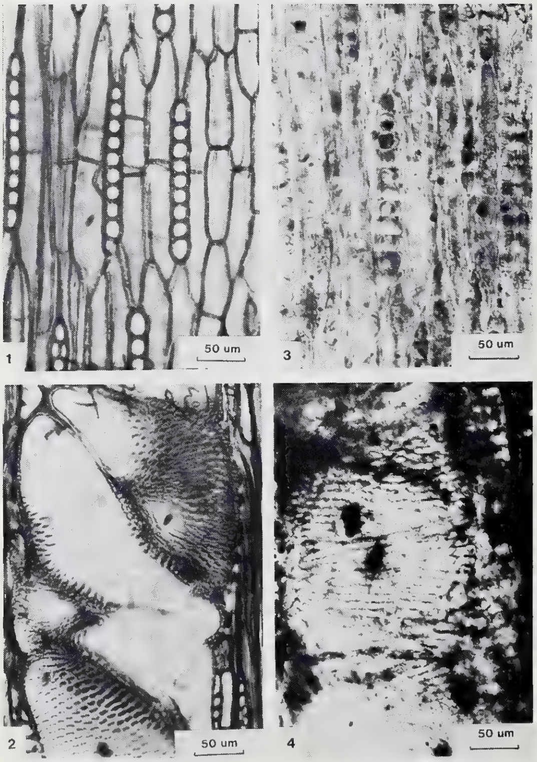

FIG. 10.—1 et 2, *Pterocarpus erinaceus* Poir. Coll. *CTFT* 6906. Sénégal. Espèce actuelle. 3 et 4, *Pterocarpoxylon tibestiense* Louvet & Boureau (1970). Coll. *Boureau* 1514A, *CFP* 548A. Eocène de la région de Ouaou en Namous. 1 et 3, coupe tangentielle montrant l'étagement des rayons et du parenchyme. Une cloison transversale sépare en deux les cellules du parenchyme; 2 et 4, ponctuations intervasculaires alternes, petites à moyennes.

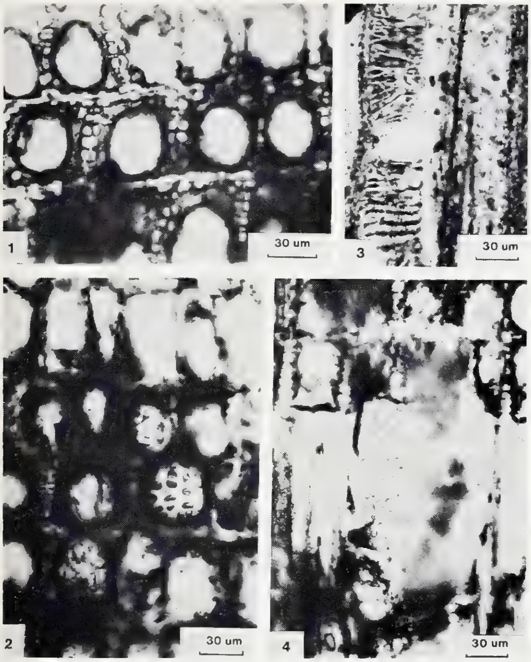

FIG. 11.—*Sonneratioxylon aubrevillei* Louvet, n. sp. Coll. *Boureau* 6475, *CFP* PA 722. Lutétien supérieur du Graret el Gifa (Libye). 1, coupe radiale montrant les ponctuations petites des cellules des rayons; 2, autre coupe radiale montrant les ponctuations de champ de croisement composées unilatéralement; 3, ponctuations vaisseaux-rayons aplaties à tendance scalariforme; 4, ponctuations intervasculaires arrondies, alternes, petites à moyennes et ornées.

dans les Argiles de Londres. On y a signalé également *Palaeowetherellia schweinfurthii* (Chandler (1954), avec *Icacinicarya youssefii* Chandler (1954), (Icacinaceae).

Les Nipaceae sont représentées par *Nipa burtinii* (Brongniart) Chandler (1954)*. Les *Nipa* se développent actuellement dans les régions très humides où l'arrière-pays est constitué par la forêt dense. Dans les couches de transition du Crétacé au Tertiaire, deux bois hétéroxylés ont été indiqués à Asselar, dans le Sahara soudanais: *Ficoxylon cretaceum* Schenk, très répandu dans le Tertiaire et *Myristicoxylon princeps* Boureau (1950). Pour Th. Monod, l'âge est Danien et A. Aubréville fait remarquer que la famille des Myristicacées n'a de représentants que dans la forêt dense humide:

(b) *Eocène.* Chandler (1954) pense que le *Nipadites sickenbergeri* Bonnet (1904) du Lutétien d'Egypte est un *Nipa burtinii* et que le *Rubiacaeocarpum markgrafii* Kräusel (1939) de l'Eocène moyen du Djebel Giuchi est également une graine de *Nipa.* Dans toute la Téthys, à la fin de l'Eocène, une diminution de la température a éliminé les *Nipa* (Germeraad, Hopping & Muller, 1968). R. Kräusel signale diverses espèces comme *Litsea engelhardtii* Kräusel (1939), Lauracée; *Ficus stromeri* Engelhardt (1907) et *F. leucopteroides* Engelhardt, (1907), Moracées; *Maesa zittelii* Engelhardt (1907), Myrsinacée; *Securidaca tertiara* Engelhardt (1907), Polygalacée.

(c) *Oligocène.* Dans l'Oligocène inférieur, on a *Quercoxylon retzianum* Kräusel (1929), *'Acacioxylon' vegae* Schenk (1888), *Atherospermoxylon aegyptiacum* Kräusel (1939) (Monimiaceae), *Ebenoxylon aegyptiacum. Combretoxylon primigenium* Louvet (1973)* et *C. geinitzii* sont Oligocène supérieur et Miocène inférieur. *Detarioxylon aegyptiacum* est pareillement Oligo-Miocène en Egypte, mais a existé dans tout le Tertiaire (Kräusel, 1939).

Néogène

Miocène inférieur. Des espèces de flore sèche décrites en Libye se retrouvent en Egypte avec *Detarioxylon aegyptiacum, Combretoxylon bussonii, Guttiferoxylon symphonoides* et *G. fareghense ?Leguminoxylon albizziae* Kräusel (1939), des *Combretoxylon* sp., *Bombacoxylon owenii, Palmoxylon aschersonii.*

Somalie

Miocène

Dans la basse vallée du Daror (Chiarugi, 1933), on retrouve *Bombacoxylon owenii* et *Detarioxylon aegyptiacum,* espèces déjà signalées. La présence d'une flore sèche tropicale au voisinage des rivages marins du Miocène ne semble donc pas particulière à la Libye. Le phénomène semble général le long des rivages du Nord de l'Afrique.

Le fait que l'on retrouve une flore sèche en Somalie, plus près de l'Equateur, laisse penser qu'il existait déjà un gradient de sècheresse de l'ouest à l'est en Afrique et il est possible que cet accroissement de sécheresse vers l'est ait commencé à l'Oligocène (Louvet, 1971, p. 193).

Pliocène

L'assèchement semble s'accentuer et certains auteurs estiment que le désert apparaît pendant cette période.

Ethiopie

Les flores tertiaires (Miocène) de la basse vallée de l'Omo ont eté étudiées par Lemoigne & Beauchamp (1972) et Lemoigne (1978) avec des Césalpiniacées: *Afzelioxylon welkitii* (L. & B.),

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* La distribution actuelle du genre *Nipa* est indo-malaise. Ce genre monotypique (*Nipa fruticans*) couvre l'Inde, la Malaisie, les Philippines, le Sud-Est asiatique et l'Australie tropicale. La répartition verticale commence au Crétacé supérieur (Ouest africain) avec un pollen épineux qu'on lui rapporte: *Spinizonocolpites baculatus.* L'apogée de *Nipa* se situe à l'Eocène où il se recontre sur les bords de la Téthys. Les *Spinizonocolpites* sont connus au Nigeria du Sénonien à l'Eocène. Il en est de même du *Proxapertites* qui présente des affinités avec les *Nipa.* Le genre *Nipa* est connu surtout par ses fruits dans l'Eocène du Bassin de Londres, en France dans les Basses-Pyrénées et l'Ile de Noirmoutiers, en Belgique et en Italie. Les fossiles du Bassin de Londres étaient vraisemblablement allochtones, c'est-à-dire résultant d'un transport par les courants marins comme le pensent Van Steenis alors que Tralau les considérait comme étant en place.

* Cette espèce est synonyme de *Evodioxylon primigenium* Kräusel (1939), devenu *Terminalioxylon primigenium* Mädel (1970) et plus tard, *Combretoxylon primigenium* Louvet (1973). De même, *Evodioxylon geinitzii* (Schenk) Kräusel (1939), est devenu *Combretoxylon geinitzii* Louvet (1973).

Brachystegioxylon welkitti (L. et B.), *B. premicrophyllum* Lakhanpal & Prakash; — Dipterocarpacées: *Dipterocarpoxylon monoteoides;* — Combretacées: *Combretoxylon desrotoris* Lemoigne (1978). *Combretoxylon* sp., *Terminalioxylon doubingeri* Lemoigne (1978); — Méliacées: *Paratrichilioxylon ludovici, Paratrichilioxylon grambastii* Lemoigne (1978).

D'autres échantillons ont été rapportés à des familles variées: Légumineuses, Papilionacées, Guttifères, Euphorbiacées, Sapotacées, Rosacées, Verbénacées, Anacardiacées, Myristicacées, Mimosacées, Moracées, Myrtacées, Burséracées et aux Monocotylédones [*Palmoxylon aethiopicum* Lemoigne (1978)]. L'ensemble correspond à une flore de savane (avec çà et là des forêts claires) et des forêts-galeries comparables à la savane actuelle d'Afrique centrale. La paléoflore du Miocène inférieur de la haute vallée de l'Omo a beaucoup d'affinités avec les paléoflores, également d'âge Miocène, d'Egypte décrite par Kräusel (1939) et du Zaïre (Lac Albert) décrite par Lakhanpal & Prakash (1970).

Tchad

Les flores ligneuses du Tertiaire et du Quaternaire du Tchad ont été étudiées en 1976 par Coppens & Koeniguer. Le climat humide du Mio-Pliocène avec des forêts denses, des forêts-galeries et des savanes boisées est prouvé par *Colaxylon coppensii* voisin de *Cola nitida, Myrtoxylon (?)kirdimiense, Afzelioxylon furonii, A. tchadense, Myristicoxylon vincentii, Leguminoxylon ouniangaense, Sapindoxylon(?)lapparenti.*

Ce climat subit un certain assèchement au Pliocène comme le prouvent la faune et la flore à *Tamaricoxylon africanum* Boureau et à restes de *Retama* proches de l'actuel *R. raetam.* L'humidité revient au Pléistocène avec à nouveau des îlots de forêts denses et de forêts-galeries avec *Caesalpinioxylon faurei,* liane caractéristique du Pliocène et du Quaternaire ancien du Tchad et d'Ethiopie.

Sénégal

En 1921, Fritel signale *Nipal* sp. aff. *N. burtinii* dans l'Eocène moyen à Bargny m'bote. En 1975, Médus fait connaitre environ 20 familles d'Angiospermes tertiaires. Parmi les pollens importants citons *Sindora* (connu depuis l'Eocène supérieur), *Spinizonocolpites* au Lutétien et *Rhizophora* dans l'Oligocène. Ces formes font penser à la mangrove. En 1978, Zaklinskaja le confirme et signale au voisinage du Cap-Vert des formations paléogènes à mangrove avec des pollens de Rhizophoracées et Sonneratiacées, *Avicennia* et *Nipa.* En outre, l'Eocène a donné *Palmocaulon monodii* Boureau & Prakash (1967), *Caesalpinioxylon tiemassaense* Koeniguer, voisin des *Schotia, Tiemassaxylon (Caesalpinioxylon?) eocenicum* Koeniguer, aux affinités incertaines, ainsi que des témoins de la forêt dense assez significatifs, *Irvingioxylon taibaense* Koeniguer (1970), voisin des *Irvingia* et un *Sapindoxylon mbaense* Koeniguer (1973), voisin des *Placodiscus,* qui sont également des arbres des forêts denses humides, semi-décidues.

Mali

Le Tertiaire du Mali oriental a donné *Bombacoxylon (Dombeyoxylon monodii* Boureau d'In Azaouad), *Myrtoxylon secretans* Boureau (Tilemsi), *Annonoxylon striatum* Boureau, *A. edengense* (S. W. de l'Adrar), *Guttiferoxylon saharianum* Boureau (N. W. de l'Adrar).

Niger

Le Mont Kanak dans le Niger oriental a donné *Opilioxylon* (Faure & Koeniguer, 1967).

Bassin de Lullemmenden (Bassin situé sur le Mali, le Niger, le Bénin et le Nigeria)

Paléogène

La végétation du Maestrichtien et du Paléogène a été décrite par Laurence Boudouresque en 1980.

(a) *Paléocène.* On y a trouvé des Nipaceae (*Inundatisporis vermiculisporites*), des Icacinacées (*Echiperiporites icacinoides*) connus dans le Miocène du Cameroun; des Onagracées *(Corsinipollenites jussiaeensis)* connues dans l'Eocène du Nigeria.

(b) *Eocène.* Dans le domaine margino-littoral et marin, on trouve des pollens hydrophiles, notamment des Filicales Schizeaceae (*Crassoretitriletes* sp.) Cyatheacées (*Cyathidites minor*), Polypodiacées *(Concavissimisporites verrucosus, Verreticulisporis* sp.)

A ces formes s'ajoute une flore de savane arborée plus continentale (*Ctenolophonodites costatus* signalé dans l'Eocène et le Miocène du Cameroun, *Bombacacidites* sp. et *Striatopollis bellus* que l'on peut rapprocher des Césalpiniacées de la tribu des Amherstiées et qui existent également jusque dans le Miocène au Cameroun et le Quaternaire au Nigeria).

Nigeria

Paléogène

Paléocène-Eocène. Au Nigeria, le groupe des *Proxapertites* (apparenté au *Nipa*) signalé pour la première fois en 1955 par Kuyl, Muller & Waterbolk dans le Paléocène est retrouvé par Germeraad, Hopping & Muller (1968) en association avec le groupe des *Spinizonocolpites.* Ils seraient tous deux limités au Paléocène et à l'Eocène. Jan du Chêne *et al.* (1978) observent ces grains de pollens associés à des Protéacées, des Myristicacées, des Bombacacées et des Convolvulacées à l'Eocène.

Néogène

Les familles Césalpiniacées, Palmiers, Convolvulacées ont été retrouvées par Legoux (1978) en association avec des Lythracées ainsi que des Lécythidacées (genre *Barringtonia*), des Césalpiniacées (genre *Brachystegia*). Au Nigeria, les Rhizophoracées, comme d'ailleurs les Composées, ne sont connues qu'à partir du Miocène, Muller (1964) (*Zonocostites scammoniae*), ce qui a permis à Germeraad *et al.* (1968) de confirmer les hypothèses de Van Steenis (1962) pour lequel les Rhizophoracées d'origine indo-malaise (où elles sont connues depuis l'Eocène) auraient migré vers l'Amérique puis vers l'Afrique. La voie de migration vers l'est aurait permis à cette famille d'atteindre l'Amérique du Sud, puis l'aire des Caraïbes pendant l'Eocène alors que l'isthme de Panama n'existait pas et où se seraient développées les espèces locales. La traversée de l'Atlantique se serait produite en début du Miocène pendant lequel les espèces américaines auraient colonisé les côtes ouest de l'Afrique.

Cameroun

Paléogène

Dans cette région ont été étudiés des macrorestes, empreintes foliaires par P. Menzel (1920), structures ligneuses par M. Dupéron (1977). Une étude palynologique par M. Cheboldaeff-Salard (1978) mit en évidence le passage du Crétacé au Tertiaire par un changement presque complet de la flore. Au Maestrichtien, la flore contient des pollens éphédroides, *Proteacidites dehaanii.* Le climat est chaud et humide à la fin du Crétacé.

(a) *Paléocène.* Suppression totale des formes du Crétacé supérieur *(Aquilapollenites, Translucentipollis, Ephedripites* et pollens de Restionacées). La flore éocène du Cameroun a livré des taxons difficiles à classer comme *Doualaidites* et *Auriculopollenites.* Dans l'Eocène supérieur, on trouve de nombreuses Dicotylédones, Ptéridophytes et surtout des Thallophytes. Cette évolution se retrouve avec des homologies qualitatives certaines dans la flore du Cameroun-Nigeria et celle du Sénégal ainsi que dans la flore sud-américaine (Colombie, Vénézuela, Trinidad) et même, mais de façon moins marquée, avec l'Inde et Bornéo.

Le changement presque complet de la flore s'accompagne d'une augmentation de *Psilamonocolpites medius* (Palmiers?), lié peut-être à un refroidissement général du globe. Encore sec au Cameroun, le climat aurait contribué à former les dépots latéritiques (Reyre, 1966).

(b) *Eocène inférieur.* Le climat est chaud mais un peu plus humide. Les Graminées seraient liées à la présence de savanes côtières tropicales. Il y a au Cameroun coexistence de plantes de milieu sec et de plantes de milieu humide. Au Lutétien, *Spinizonocolpites* (apparenté à *Nipa*) qui indiquerait la mangrove, coexiste avec *Bombacacidites,* plus nettement tropophile (Croizat, 1952) comme au Sénégal.

(c) *Eocène supérieur et Oligocène.* Le climat chaud devenant humide, entraîne un grand développement de Ptéridophytes, avec Champignons. La flore d'Angiospermes se diversifie. C'est la forêt dense, humide et connue actuellement avec son cortège de Dicotylédones arborescentes, lianescentes, épiphytes et parasites, de Ptéridophytes et de Thallophytes.

L'Oligocène a été mis en évidence grâce à *Cicatricosisporites dorogensis* (Schizéacée, cf. *Anemia* ou *Mohria*) et *Magnastriatites howardii* (Parkeriacée, cf. *Ceratopteris cornuta*). Certain dans le Bassin du Sénégal et dans l'Ouest marocain, l'Oligocène semble absent de la Côte d'Ivoire, mais on trouve au Nigeria ces deux mêmes formes, pareillement dans l'Oligocène.

Néogène

Le genre *Sindora,* connu au Sénégal à l'Eocène supérieur se retrouve au Cameroun à l'Oligocène et au Miocène.

Une Flacourtiacée tertiaire (*Casearioxylon tibatiense* Dupéron-Laudoueneix (1977), voisine des *Casearia* de savane boisée ou forêt dense) a été signalée près de Mbakaou. Au Cameroun, une palynozone à *Verrutricolporites rotundiporis* caractérise le Miocène inférieur (ee tacon correspond à une Lythracée: *Crenea* ou *Rotala*).

Kenya

Dans la série détritique des grès néogènes du Turkana, à l'ouest du Lac Rodolphe, ont été recueillis de nombreux bois silicifiés parmi lesquels on a identifié des plans ligneux d'*Euphorbioxylon, Xylopioxylon, Afzelioxylon: Andiroxylon biseriatum* (Papilionacées) et une Loganiacée (Delteil & Koeniguer). Le genre *Dipterocarpoxylon* (avec *D. africanum* Bancroft, 1935) est actuellement indomalais. Décrit dans le Néogène du Mont Elgon, sa détermination est essentiellement fondée sur l'appareil sécréteur qui le rapproche des *Dipterocarpus* et l'éloigne des *Monotes* d'Afrique. Miss Bancroft (1935) eut l'idée de pulvériser un fragment de ce bois silicifié et d'extraire les secrétions des éléments conducteurs avec de l'éther. Cette manipulation ancienne est importante. Elle a ouvert un champ nouveau aux investigations sur les bois fossiles. On peut parfaitement extraire par chromatographie en phase gazeuse les complexes oléo-résineux des bois minéralisés ou non, bien conservés dans certains cas, malgré leur ancienneté, permettant ainsi de confirmer les déterminations fondées sur l'anatomie.

La présence de ce *Dipterocarpus* en Afrique se trouve confirmée par la découverte de feuilles dans les grès de Nubie, *Dipterocarpaceophyllum hirmeri, D. zeraibense* (Seward, 1935). D'autres bois fossiles: *Dipterocarpoxylon giubense, D. scebelianum, D. somalense* (Chiarugi, 1933), proviennent de Somalie.

Le Miocène du Mont Elgon a également livré des bois fossiles signalés par Chaney (1933): *Banksia, Berlinia, Cassia, Olea, Parinari, Pittosporum, Terminalia.*

CONCLUSION

Mise en place des forêts africaines actuelles

L'assèchement progressif de la flore dans le nord de l'Afrique au Tertiaire se comprend si l'on tient compte de la régression des mers épicontinentales vers le nord et de la dérive du Continent africain. L'équateur se trouvait apparemment 10° plus au nord (1 000 km) à la fin de l'Eocène inférieur. Il était situé encore plus au nord au début du Paléocène et des mers épicontinentales s'étendaient alors bien plus au sud. La partie nord de l'Afrique paléocène devait se trouver en pleine zone équatoriale, ce qui permet d'expliquer la présence d'*Entandrophragmoxylon normandii* dans le Paléocène du Tinrhert et celle de *Nipa burtinii* dans le Dano-Montien d'Egypte, de *Trichilioxylon russel-*

lii Koeniguer dans le Paléocène du Niger. La montée du Continent africain vers le nord entraîne un déplacement de l'équateur vers le sud (*Pterocarpoxylon arambourgii* Boureau, en bordure du golfe yprésien du Tadla est proche des *Pterocarpus* actuels), et à l'Eocène moyen on trouve des formations humides en bordure de la Mésogée, bordées au sud par une flore plus sèche: la zone équatoriale se trouve plus au sud; *Nipadites* sp. aff. *N. burtinii* est Eocène moyen dans le Golfe du Sénégal. Dans l'Eocène du Sénégal, Koeniguer a décrit des bois fossiles proches d'arbres des forêts denses tropicales, comme *Placodiscus, Irvingia* et *Schotia.*

On aurait, dès cette époque, une zone à flore sèche comprise entre une zone de forêts plus humides bordant la Mésogée au nord et une autre correspondant à la zone équatoriale au sud.

La montée du Continent ajoutant ses effets à ceux de la régression des mers épicontinentales, le biotope moins humide va prendre de plus en plus d'importance à l'Eocène supérieur et à l'Oligocène. Corrélativement, les formations denses au bord de la Mésogée vont régresser et disparaître pour faire place à une flore plus sèche au Miocène inférieur [Libye, Egypte, Sahara occidental (Rio de Oro) et vraisemblablement Tunisie].

Cette végétation va disparaître à son tour au cours du Néogène des régions du Nord de l'Afrique, mais il s'agit probablement d'une restriction d'aire plutôt que d'un véritable mouvement vers le sud, car les formations à *Combretoxylon (Anogeissuxylon) bussonii* et à *Detarioxylon aegyptiacum* ont dû être présentes au nord de la bande équatoriale pendant tout le Tertiaire.

Par contre, l'équateur occupe une position plus méridionale voisine de la position actuelle et la palynologie permet de conclure qu'au Miocène la forêt dense était bien en place dans le bassin sédimentaire de Douala (Cameroun).

De même, Lakhanpal & Prakash (1970) ont signalé dans le Miocène du Zaïre, *Brachystegioxylon premicrophyllum, Isoberlinioxylon congoense, Carapoxylon cahinii*[*] rapproché d'*Entandrophragma candollei,* Méliacée de forêt dense; Les deux autres espèces sont à rapprocher d'espèces actuelles vivant dans les forêts claires du Zambèze.

Voulant préciser le milieu naturel dans lequel les Primates pouvaient vivre au Fayoum, Kortlandt (1980) arrive à la conclusion que l'écosystème du delta à l'Oligocène est de type sahélien (la présence de racines de diamètre maximal de 4 cm le montrant) et formé de buissons avec ou sans petits arbres.

Il pense que la grande forêt supposée à l'Oligocène par Louvet et 'estimée à 150 km d'épaisseur' n'a jamais existé. Cette affirmation résulte d'une interprétation hâtive d'une carte synthétique (Louvet, 1971: 499,2) ayant pour but de montrer la régression et la disparition de la forêt dense au cours de l'Oligocène, qui a pu être plus rapide en certains points (*l.c.* 190, 430).

Ces faits sont d'ailleurs mis en évidence par un pointillé sur la carte citée, non seulement à l'est, mais à l'ouest du Golfe de Syrte (*l.c.* 407). Il a été souvent signalé que ces formations devaient être réduites et que seules des études régionales nouvelles pourraient apporter les précisions nécessaires (*l.c.* 407). Par ailleurs, les lignes de séparation des zones dans ce schéma n'est pas une véritable frontière (*l.c.* 212) et il est logique de penser que la forêt dense avait une répartition discontinue, la "savane" pouvant même atteindre localement la mer (*l.c.* 199).

En réalité, on n'a jamais pu affirmer qu'il existait une forêt dense de 150 km d'epaisseur en Egypte, à l'Oligocène. Il n'y a donc pas d'opposition fondamentale entre les conceptions de Louvet et celles de Kortlandt, la forêt dense oligocène étant en régression très nette (la date de sa disparition reste à trouver) et avec une répartition discontinue interrompue par endroits notamment par des dépots deltaiques de grands troncs transportés par des fleuves et appartenant d'ailleurs à une flore sèche *(Detarioxylon aegyptiacum, Combretoxylon).*

Ces troncs flottés peuvent cependant coexister avec de grands troncs de forêts-galeries proches de la zone deltaïque (une Monimiacée, *Atherospermoxylon aegyptiacum* Kräusel 1939, a été identifiée dans l'Oligocène inférieur en Egypte). Il est possible aussi que l'on retrouve dans le grand delta oligocène du Fayoum des racines ayant un diamètre supérieur à 4 cm.

Kortlandt semble considérer que son écosystème est resté invariable pendant tout l'Oligocène, écartant toute variation des rivages marins et toute modification climatique, ce qui parait excessif.

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[*] Les *Carapa* ayant des rayons plus hétérogènes, ce bois doit être rangé dans le genre *Entandrophragmoxylon* et appelé *Entandrophragmoxylon (Carapoxylon) cahinii* (Louvet, 1971: 440).

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The Late Quaternary history of climate and vegetation in East and southern Africa

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ABSTRACT

In the vast region of East and southern Africa the alternating glacial and interglacial periods of the Quaternary were characterized by considerable changes in temperature and precipitation. During the last glacial maximum the influence of the ITCZ was limited, while the circulation systems were strengthened. The ocean surface waters were cooler and the Benguela Current was activated. In the montane areas of East Africa and also in southern Africa the temperature dropped by about 6°C.

During this hypothermal period, rainfall on the east African plateau and mountains diminished. Summer precipitation could still penetrate the eastern half of southern Africa from the Indian Ocean, while the western half was arid to semi-arid. Cyclonic winter rain migrated further north beyond the latitude of the Orange River.

The consequences of these climatic changes during the last glacial maximum were that the woodlands of East Africa opened up. On the plateau of South Africa austro-afroalpine vegetation dominated. The south coastal plain was very windy and cold to temperate, while the Namib and Kalahari were respectively hyper-arid and semi-humid.

During hyperthermals the vegetation pattern resembled present-day conditions more closely.

RÉSUMÉ

HISTOIRE DU CLIMAT ET DE LA VÉGÉTATION À LA FIN DU QUATERNAIRE DANS L'EST ET LE SUD DE L'AFRIQUE.

Dans la vaste région de l'Afrique méridionale et orientale, les périodes glaciaires et interglaciaires du Quaternaire furent caractérisées par des changements considérables de température et de précipitations. Durant l'apogée de la dernière période glaciaire, l'influence du ITCZ fut limitée, tandis que les systèmes de circulation se renforcèrent. Les eaux de surface de l'océan devinrent plus froides et le courant du Benguela entra en activité. Dans les régions montagnerdes de l'Afrique de l'Est et aussi en Afrique méridionale, la température tomba d'environ 6°C.

Pendant la période hypothermique, la pluviosité sur les plateaux et les montagnes de l'Est africain diminua. Les précipitations d'été pouvaient encore pénétrer dans la moitié est de l'Afrique méridionale à partir de l'océan Indien, tandis que la moitié ouest était aride à semi-aride. Les pluies cycloniques d'hiver émigrèrent vers le Nord, au delà de la latitude de fleuve Orange.

Les conséquences de ces changements climatiques pendant l'apogée de la dernière période glaciaire furent que les forêts claires de l'Est africain devinrent plus ouvertes. Sur le plateau de l'Afrique du Sud, la végetation austro-afroalpine devint dominante. La plaine côtière sud fut très venteuse et froide à tempérée, tandis que le Namib et le Kalahari furent respectivement hyper-aride et semi-humide. Durant les périodes hyperthermiques, la physionomie de la végétation s'est davantage rapprochée de son aspect actuel.

INTRODUCTION

The part of Africa under discussion in this article forms a vast uplifted plateau delimited towards the oceans by raised escarpments. In Tertiary times two major periods of tectonic uplift occurred, namely in the end Miocene and terminal Pliocene, the last one of which raised the interior plateaux by about 1 000 m (King, 1978).

In east to west cross section central and southern Africa have the appearance of an enormous flat dish with a slightly raised margin. Important depressions in the surface of this dish are the early Tertiary Congo and Kalahari basins and others situated in the Karoo, the Transvaal and the river valleys of the Limpopo and Zambesi.

The high and steep monoclines of central and southern Africa, delimiting the Pliocene coastal plains from the much older interior, cut off the oceanic influence and consequently caused the southern basins to become dry and warm.

In Plio-Pleistocene times rift valleys developed in the upwarped ridges separating the basins. These elongated new valleys and the many volcanoes which were built upon their margins added to the varied topography and climate.

The vast region stretching from Kenya and Uganda down to the Cape of Good Hope has during the Quaternary witnessed impressive changes in climate and vegetation. Warmer and more humid conditions encouraged the spread of forest, woodlands and savanna. Colder and drier climates favoured enormous migrations in the reverse direction. During the Quaternary these processes have been repeated many times with different intensities, but we can only trace them with some degree of accuracy for the last 30 000 years.

The evidence for these dramatic changes of the face of Africa is provided by multidisciplinary studies. This approach has over the last twenty years provided an acceptable general model for the changes which took place although very many details remain to be cleared up.

It is convenient to separate the discussions on East and southern Africa as they represent different

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biotic and climatic regions. The part on East Africa will concentrate mainly on Kenya, Uganda and Tanzania and for southern Africa the emphasis will be laid on South Africa and Namibia as these countries have been studied in more detail than the intervening region. Moçambique will not be discussed.

EAST AFRICA

Present climate and vegetation

East Africa would in general be a semi-arid to arid part of the world if it did not have its many mountain ranges, hills and volcanoes which catch orographic rainfall. The eastern sector is under the influence of the alternating NE and SE monsoons. The SE monsoon has the longest trajectory over the ocean, but the air flow is shallow and divergent and does not meet a high coastal mountain range so that it brings only little rain to the vast plateau of the interior.

The other main source of rainfall is the monsoon which penetrates equatorial Africa from the Atlantic Ocean and loses most of its humidity over the Zaire basin and on the high mountain ridge bordering the western Rift Valley.

In the course of the last 1 000 years man has had a devastating influence on the vegetation by destruction of forest, burning woodlands and overgrazing. It would, however, be an over-simplification to assume that without human interference East Africa would have been completely covered by forest. The opening up of the vegetation is of much older age

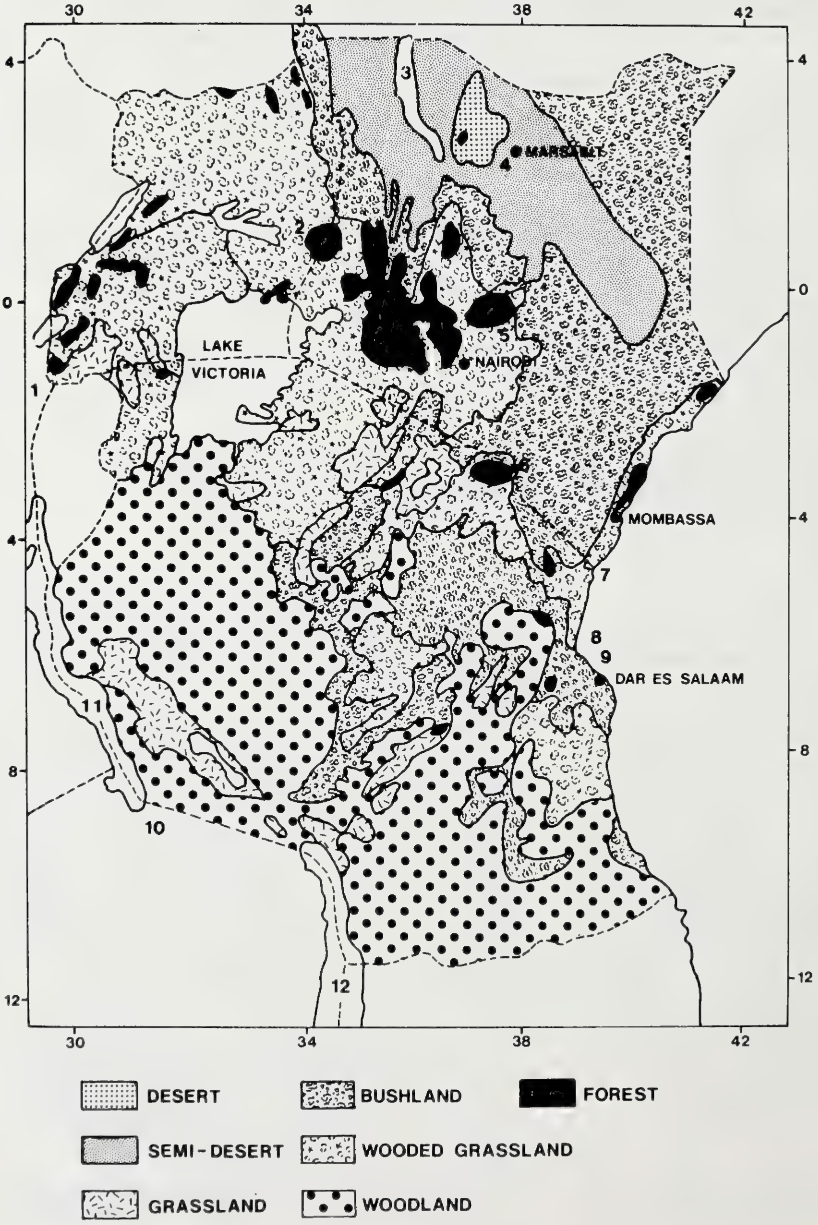

FIG. 1.—Vegetation of East Africa.

and is the consequence of the gradual desiccation of Africa which started at least during the world wide cooling in the end of the Miocene (5 My). This is also testified by the fauna of alcelaphine antelopes which are highly adapted to this open type of vegetation (Vrba, 1979, 1980).

The vegetation pattern of East Africa is one of the most varied of the world ranging from lowland rain forest with an equable warm and humid climate to sun parched semi-desert and to the highest mountains in Africa which are covered with residual glaciers right under the equator. This pattern is primarily arranged according to the availability of water. (Fig. 1).

Late Quaternary changes in East Africa

In reconstructing the Late Quaternary changes we will limit ourselves mainly to the two extreme periods known in this time span, *viz.* the hypothermal or last cold maximum and the Holocene Climatic Optimum.

During the last glacial maximum c. 18 000 yr B.P. the tropical oceans, which provide the humidity of East Africa, were colder than at present. The average ice-age zonal sea surface temperature for the entire Indian Ocean was 1,4–1,5°C cooler (Prell & Hutson, 1979). The tropical part of the Atlantic Ocean was 4–5°C colder than at present (Morley & Hays, 1979). Flohn & Nicholson (1980) calculated that, as a consequence of this, the evaporation over the tropical oceans of the world was reduced to 25–30% of the normal value. This 'ice-age aridity' can also be inferred from the low levels of practically all the lakes in tropical Africa (Van Zinderen Bakker, 1972; Butzer *et al.*, 1972). It affected nearly the whole of Africa except for the northern (Rognon, 1981) and the southern (Van Zinderen Bakker, 1976) extremities.

During the last glacial maximum the wind speed in the Northern Hemisphere was in summer accelerated by 124% and in winter by 24% (Newell *et al.*, 1981).

The lowering in temperature and the dryness of the climate were proved by pollen analytical studies of some six palynologists who worked on the East African mountains in the short period of 1961–1971 (Livingstone & Van der Hammen, 1978). Since then, very few pollen diagrams have been published from this region, but the continued interest of A.C. Hamilton in tropical palynology has done much to assess and interpret the ecological and biogeographical aspects of the data that had been collected.

The first interpretations inferring a cold and dry climate were made by Coetzee (1964, 1967) and Van Zinderen Bakker (1962, 1964), who studied pollen sequences from the Cherangani Hills and Mt Kenya. Their conclusions were based on evidence from various pollen types amongst which grass pollen played an important part. This interpretation has been criticized by Livingstone (1967) on the grounds that grass pollen in these mountains is not a valid indicator for a cold alpine environment. The climatic changes indicated by these diagrams have been re-assessed by Van Zinderen Bakker & Coetzee (1972) and by Hamilton (1974b) without taking the grass pollen into account. These new interpretations, based on studies of Hamilton (1972) on pollen deposition in the Ugandan mountains, did not change the original conclusions, *viz.* that during the last glacial maximum the climate was dry and c. 6°C colder than at present. It is strange that the use of grass pollen by Van Zinderen Bakker and Coetzee is still being attacked 'post mortem' by Livingstone (1975, 1980).

Similar results with pollen sequences have been achieved with cores from Uganda by Morrison (1968) in the Rukiga Highlands in south-west Uganda where the climate was dry and the mean annual temperature was 18 000 yr B.P. also c. 6°C lower than now. Livingstone (1967) originally explained his results in the Ruwenzori in a different way, but the re-interpretation by Hamilton (1972) came to conclusions which are practically identical to those from Kenya and the Rukiga Highlands for the last 15 500 years. More important proof for dryness on the African plateau was provided by Kendall (1969), who showed that the area round Jinja on the northern edge of Lake Victoria, where at present lowland forest is dominant, was occupied by an open arid savanna between more than 14 500 and 12 000 yr B.P.

Coetzee (1967) has designated the last cold and dry period after the type-site, the *Mount Kenya Hypothermal.* This cold maximum was coeval with the last severe maximum of the European Würm glaciation. During this time the vegetation belts on the East African mountains shifted 1 000–1 100 m downward. Similar changes have been recorded in the equatorial Andes by Van der Hammen & Gonzalez (1960).

In East Africa, the consequences of the colder and drier climates were dramatic. We will first look at the forest and the mountain vegetation. The lowland forest, being most sensitive to drought, will in tropical Africa probably only have survived in the following four areas: West Africa (west of the Togo/Dahomey gap), Cameroon/Gabon, E. Zaire and along the East African coast (Hamilton, 1974a, b; Diamond & Hamilton, 1980). The position of the refuges is also indicated by the distribution of forest mammals (Kingdon, 1971) and of endemic species of forest passerine birds (Diamond & Hamilton, 1980).

The three vegetation belts occurring on many mountains above the moist montane forest, *viz.* the dry montane forest, the Ericaceous Belt and the Afroalpine Belt, persisted at much lower altitude during the hypothermal period. The remarkable small biota of the Afroalpine Belt with their high degree of endemism remained isolated on the highest parts of the mountains and could not make contact via the lowlands. This also applies to the montane forest of the various mountains.

The opening up of the vegetation of Africa during the hypothermal period may have provided a migration route between the arid north-eastern part of East Africa and Namibia for plant and animal taxa adapted to dry conditions (*Palaeoecology of*

Africa, vol. 1, 1963, p. 188/9, vol IX 1969, chapter VI). An 'arid corridor' of this type will develop when the present rainfall diminishes and this corridor will run in a SW-NE direction passing between the lakes Tanganyika and Malawi (Van Zinderen Bakker, 1969a, b). Until some ten years ago, when the glacial periods were generally supposed to have had a wet climate, this corridor was supposed to have been of interglacial age. Hamilton (1974b) suggested that it is well possible that a connection of this kind was open or partly open at various intervals to migration during the dry period before 12 000 yr B.P.

The data on conditions on the plateau of East Africa during the hypothermal period are very scanty. The pollen record of Pilkington Bay (Kendall, 1969) and of Cherangani (Coetzee, 1967; Hamilton, 1974b) and also the low lake levels indicate that the climate was certainly dry.

The glaciation on the East African mountains came to an end some 15 000 years ago, at the same time as the Würm Glaciers in Europe and the Wisconsin counterparts in America started to wane (Livingstone, 1962). The gradual warming of the climate only had a marked effect on the vegetation near 12 600 yr B.P. at a time coeval with the Bölling-Alleröd Interstadials in Europe. The consequence of this warming up was that evaporation of the world's oceans was activated so that more moisture could reach tropical Africa from the Atlantic and Indian oceans. From that time onward, forest developed along the northern boundary of the Victoria Basin. Hamilton (1981) could show that the forest elements spread from the refuge along the western Rift Valley in an eastern direction probably mostly by long distance dispersal. At about 10 500 yr B.P., the temperature in the mountains had reached the present level. After a minimum around 10 200 B.P., very high lake levels were reached between 10 000 and 7 500 yr B.P. At about 4 600–4 000 yr B.P. the temperature in the mountains was higher than at present and the forest expansion at Pilkington Bay reached its maximum.

SOUTHERN AFRICA

Present climate and vegetation

The vegetation of southern Africa gives a very accurate image of the climatic pattern of the subcontinent. The climate is mostly arid to semi-arid and would, as in East Africa, have been drier if it was not for the orographic rainfall received by high mountains. The rainfall in the tropical part of Africa south of the equator has a zonal pattern caused by latitudinal migration of the ITCZ which follows the sun and is therefore summer rainfall. The vast zone of woodland, covering eastern Angola, Zambia, Malawi and most of Moçambique receives this precipitation which amounts from 600–800 mm per year. This rainfall pattern changes suddenly south of 20°S where the isohyets run more or less in a meridional direction. Further south the following circulation and rainfall systems dominate southern Africa (Van Zinderen Bakker, 1976):

—the mid-latitude westerlies bring cyclonic winter rain to the S.W. Cape.

—subtropical anticyclones are centred on 30°S. The stable and strong high situated near the Namibian coast over the South Atlantic produces a subsiding, divergent wind flow and is one of the main reasons for aridity in the western half of the subcontinent.

—the Benguela Current with its accompanying cold upwelling runs parallel to the Namibian coast as far north as Cape Frio and prevents moisture from penetrating the continent.

—summer rainfall reaches the interior from the Indian Ocean in an anti-clockwise airflow.

—the warm Agulhas Current along the east and south coast brings much moisture to the coastal region and the north-eastern interior.

The present-day vegetation of southern Africa presents textbook examples of extensive ecological gradients, especially on the plateau in a south-northerly and a west-easterly direction. From south to north we find the semi-arid Karoo with a BWk-climate giving way in a northern direction to grassland of the southern Highveld and the open savanna of the Kalahari basin (BSh-climate). Further north the *Brachystegia–Julbernardia* zone, with a warm Cwa-climate, runs obliquely across the continent.

In a west to east direction, the gradient is even more impressive as it is of an orographic, geological and ecological nature. The hyper-arid erg of the southern Namib Desert (BWk-climate) gradually grades in an easterly direction into the Kalahari savanna (BSh-climate). Still further east the open *Cymbopogon–Themeda* grassland covers the southern Highveld which above an altitude of c. 2 250 m is replaced by the austro-afroalpine grassland of Lesotho.

The eastern and southern coastal plains of the subcontinent form a different ecological region and conditions range in a south to north direction from temperate to tropical. The fynbos region of the SW Cape has a winter rainfall Csb-climate. This changes to an equatorial winter dry climate (Aw) of the tropical Moçambique plain. The transition from temperate to tropical biota occurs at 28° 5'S. Lat. near Lake St Lucia.

Late Quaternary changes in southern Africa

Important information about temperature changes has become available from oceanographic and terrestrial evidence especially for the last glacial maximum around 18 000 B.P.

Drastic decreases in temperature occurred in the Antarctic region, although the changes in the oceanic environment south of Africa were not very pronounced. The CLIMAP-map shows an anomaly area of more than −4°C along the south-eastern coast of South Africa (CLIMAP 1976). The Benguela Current and its cold upwelling lowered the temperature 2–5°C and penetrated much further north (Van Zinderen Bakker, 1967; De Ploey, 1969; Bornhold, 1973; Giresse, 1978). The Agulhas Current was a weak tropical current in summer and in winter was replaced by cool waters (Hutson, 1980).

Undated periglacial phenomena in the high Drakensberg, on screes and in caves along the south coast (Harper, 1969; Butzer, 1973) indicate decreases in temperature of as much as 3,5–10°C, whereas in the Wolkberg Cave well dated lowering in temperature amounted to 8–9,5°C (Talma *et al.*, 1974).

During this cold period the anticyclones were strengthened and the wind speed was accelerated by 17% (Newell *et al.*, 1981). The oceanic circulation was also intensified.

(a) *30 000–13 000 B.P.*

In recent years the following information has become available on the consequences of these climatic changes in South Central and Southern Africa. At Kalambo Falls (8° 30′S) near the south-eastern corner of Lake Tanganyika a number of isolated pollen samples show that during the 'Kalambo Interstadial' from c. 30 000 to c. 27 000 yr B.P. the climate was slightly warmer and wetter than today (Van Zinderen Bakker, 1969a). During the last cold maximum, which followed. The *Brachystegia* woodland opened up which may indicate the existence of an arid corridor. The temperature was then about 4°C lower than at present. The 22 000 year old pollen record from Ishiba Ngandu at c. 12°S on the plateau of Zambia does, however, not give information on such changes in the woodlands (Livingstone, 1971).

The history of the *Acacia-Commiphora* savanna of the Kalahari further south may more or less have followed the pattern of the Kalambo Falls sequence. During a time which immediately followed and probably overlapped with the Kalambo Interstadial the Kalahari received much rainfall which also penetrated the eastern part of Namibia and episodically even the Namib Desert proper (Heine, 1980, 1981, 1982). Lake Palaeo-Makgadikgadi gained a very high stand and tropical savanna and woodlands must have been spreading southward. During the period from 39–28 000 B.P. even the Namib Desert received more rainfall. From 28 000 to c. 25 000 B.P. rainfall increased in the catchment area of the Kuiseb River and decreased between 23 000 and 19 000 B.P. (Vogel, 1982).

During the subsequent colder period which, according to Heine (1981), lasted from 19 000–13 000 B.P., only episodically small lakes developed in the Makgadikgadi depression (Heine, 1982). Strong winds inferred from the alignment of the dunes indicate that during the last cold maximum the anticyclone over the interior was larger or had a more northerly position compared with today (Lancaster, 1979, 1981). The Kalahari and the central part of southern Africa received limited summer rainfall. This rain was generated by eastern winds drawn in from the Indian Ocean by the strengthened overland anticyclone. The drier, colder and more windy climate will have opened up the woodlands and savannas and diminished the tropical influence while drier floral elements will have invaded the Kalahari from the south.

In the southern Kalahari a more humid climate prevailed in that in winter the summer rainfall was replaced by precipitation originating from the northward displaced westerlies (Heine, 1980, 1981, 1982). The consequence of this evenly distributed low rainfall was that the Molopo could at certain times become a perennial river *(ibid).*

These subhumid conditions of the southern Kalahari can be correlated with the impressive climatic chronology described for the Gaap Escarpment, according to which the climate during phase Vc was subhumid from ⩾ 21 000 to 14 000 B.P. (Butzer *et al.*, 1978). Before and after this more humid phase, a lower temperature is inferred from the stratigraphic evidence of the Gaap Escarpment. The dating of the older of these colder periods is not yet quite certain, but it is not well possible that it coincided with the warmer Kalambo Interstadial. The subhumid conditions must have encouraged the spread of savanna vegetation. So far no evidence from fossil pollen is available for this period.

From the fossil pollen record of the thermal spring deposits at Wonderkrater further to the east (24° 26′S), it can be concluded that during the period of c. 30 000 to c. 26 000 B.P. the climate may have been cool-temperate and the humidity did not vary much from the present semi-arid to subhumid conditions (Scott, 1982). During the last cold maximum cooler and moister conditions prevailed similar to those at present known from the lower part of the austro-afroalpine zone in Lesotho. The bushveld had changed into grassland with alpine and fynbos elements (Scott & Vogel, 1978).

A similar situation occurred on the plateau of the Orange Free State where the temperature had decreased 5–6°C (Van Zinderen Bakker, 1976). This will have caused a downward shift of the austro-afroalpine grassland of the Malutis of about 1 000 m so that the 'cold' grassland probably invaded the plateau of the Orange Free State and the surroundings. The montane forests of the valleys and ravines will have disappeared and above the altitude of 3 000 m no vegetation existed (Van Zinderen Bakker & Werger, 1974). Cottrell (1978) explains the present distribution of the southern African butterflies as a consequence of these shifts of vegetation.

The little information which is available suggests that during the Kalambo Interstadial summer rainfall could penetrate part of the Namib Desert (Heine, 1982). The climate became arid during the ensuing last cold maximum especially in the middle and northern Namib. The South Atlantic anticyclone was strengthened and strong southerly winds moved the longitudinal dunes. The Benguela Current aggravated the aridity further northward. The possibility that the westerlies could bring winter rain in the southern erg to c. 24° S. Lat. as to the southern Kalahari is still considered (Van Zinderen Bakker, 1976).

The composition of the Namib flora shows that as many as 34,5% of the species have a restricted distribution or are endemic (Robinson, 1978). The majority of these species occur in the winter rainfall area of the southern erg which points to isolation in a wide variety of habitats (Seely, 1976, 1978).

(b) *13 000 B.P. – the present*

Conditions in southern Africa changed significantly in late glacial times, especially round 13 000 yrs B.P., when the climate became warmer. At Ishiba Ngandu in Zambia such changes could, however, not be revealed by pollen analysis (Livingstone, 1971). Further south more summer rainfall reached the subcontinent. In the Kalahari these warmer and more humid conditions caused a southward migration of tropical vegetation. In the North, Lake Makgadikgadi filled up again. However, the southern region along the Orange River became semi-arid to arid (Butzer *et al.*, 1978) as the summer rains from the Indian Ocean and the cyclonic winter rain no longer reached this region. The Namib Desert, similarly, was a no-man's-land as far as rain was concerned. At Wonderkrater an important climatic change occurred at c. 12 000 B.P. The open vegetation changed to bushveld as the climate became semi-arid and cool-temperate (Scott, 1982).

During the early Holocene the temperature rose further and summer rain penetrated the subcontinent at least as far as the Orange River region (29° S. Lat.). Heine (1982) described wetter climates for the southern Kalahari (9 000–8 000 yrs B.P.) and the western Kalahari (8 705 ±165 yrs B.P.) and points out that this data fits well with slightly more humid conditions even in the southern Namib desert at Mirabib from c. 8 500–8 000 B.P.

Pollen studies at Wonderwerk Cave (Van Zinderen Bakker, in preparation) have shown that an open savanna of subtropical affinity developed in this region between 9 000 and 5 000 B.P. Subhumid conditions also existed in the Gaap Escarpment between 9 700 and 6 500 B.P. (Butzer *et al.*, 1978). In the area where the Harts, Vaal and Orange Rivers join similar conditions have been inferred by Butzer *et al.* (1979). The poorly dated member IV of the Riverton Formation also fits in this wetter episode (Butzer *et al.*, 1973; Helgren, 1978).

This early Holocene period must have been the Climatic Optimum for this region when summer rain penetrated southward at least as far as 29° S. Lat. This rain did not reach Aliwal North on the Orange River further east at 30° 19'S. Lat. as is shown by the pollen studies of Coetzee (1967). Round 9 600 yrs B.P. the climate at this site was arid.

The timing of the Climatic Optimum fits well with oceanographic evidence. In the northern Cape Basin at 25° 30'S. off the coast of Namibia the warmest temperature within the Holocene occurred at 7 000 yrs B.P. (Embley & Morley, 1980).

The climate of the early Holocene at Wonderkrater differed from the conditions described so far as it was warm and semi-arid. The surroundings of the site were occupied by Kalahari thornveld (Scott, 1982). It may well be that the anticyclone was then situated near this site.

The climatic evolution of the middle and late Holocene is not well known for southern Africa. During the middle Holocene an arid period occurred (Wonderwerk 5 000–c.3 000B.P.; Gaap 6 500–4 500 B.P.; Orange-Vaal-Hartz region about the same time as at Gaap). The climate then became subhumid with minor drier intervals in this region. The explanation of these changes requires more knowledge about palaeotemperatures, evaporation and precipitation and former vegetations.

(c) *The Cape coastal region*

This region is dominated by the westerlies especially in its western part. During colder periods this influence will have been aggravated so that the southwestern Cape received more winter rain. The southern Cape coastal region probably had a different history. Many different disciplines have provided information on the palaeoenvironments of this region (Martin, 1968; Klein, 1972, 1974; Dingle & Rogers, 1972; Schalke, 1973; Van Zinderen Bakker, 1976; Deacon, 1979). The cold glacial maxima were characterized by a low sea level, very large emerging coastal plains, a fairly cool and very windy climate and consequently an open vegetation with much grassland in which grazers such as quagga, wildebeest and springbok roamed. The adjoining colder ocean must have been responsible for a fairly dry climate. The archaeological and especially the faunal remains excavated in the many coastal caves provide important evidence for these palaeoenvironmental conditions. When the climate ameliorated from 13 000–12 000 yr B.P. onward, the sea level rose substantially, the temperature attenuated and wind force diminished so that the open grassland was replaced by a closed vegetation which supported a completely different fauna.

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Histoire de la végétation et du climat de l'Afrique nord-tropicale au Quaternaire récent*

J. MALEY**

RÉSUMÉ

L'examen critique des données polliniques disponibles concernant la végétation saharienne permet de conclure qu'elle n'a subi que peu de changements qualitatifs au cours des vingt derniers millénaires. Il faut essentiellement noter une certaine transgression sur le Sahara des taxons tropicaux de type sahélien vers le milieu de l'Holocène Quantitativement, quelques données polliniques et géologiques convergent pour indiquer que les plaines sahariennes ont été extrêmement arides entre 20 000 et 15 000 ans BP environ et que sur les montagnes la végétation s'est beaucoup raréfiée. Une certaine recolonisation s'est effectuée à partir de 15 000 ans BP sur les montagnes.

L'étude pollinique de l'Holocène du Bassin du Tchad à Tjéri, vers le centre du bassin, met en évidence un changement majeur vers 7 000 ans BP, caractérisé en zone sahélienne par une brutale extension des taxons arborés jusques vers 5 000 ans BP, correspondant probablement à une extension de la savane sahélienne. Un changement important est intervenu aussi à la même époque sur les zones soudanienne et soudano-quineénne où s'est produite en particulier entre 7 000 et 4 000 ans BP une extension de certains taxons qui se développent actuellement sur les sols bien drainés des interfluves.

Un tel changement vers 7 000 ans BP se retrouve aussi lorsqu'on examine les diverses données stratigraphiques, sédimentologiques et pédologiques disponibles pour l'Afrique nord-tropicale. En particulier, on observe qu'entre 15 000 et 7 000 ans BP la sédimentation était essentiellement de type argileux avec sur les interfluves le développement d'une pédogenèse de type vertisolique (montmorillonite dominante), tandis qu'après 7 000 ans BP la sédimentation est devenue plus grossière, de type sableux, avec sur les interfluves le développement d'une pédogenèse de type ferrugineux tropical (kaolinite dominante).Il apparaît que le changement marqué de type de sédimentation a correspondu à un changement hydroloqique majeur et qu'en particulier le dépôt des sédiments sableux plus grossiers doit être associé à des crues brutales comparables aux crues actuelles.

L'interprétation paléoclimatique de ces données nécessite tout d'abord une connaissance précise de la climatologie dynamique actuelle de ces régions. Il faut ainsi distinguer les pluies qui se forment au sein de la mousson de celles qui se forment plus au nord sur la zone tropicale et particulièrement, au Sahara central. Ces dernières dépendent de dépressions qui sont engendrées par le 'Jet Stream Subtropical' et dans lesquelles la vapeur d'eau précipitée est d'origine équatoriale. Du fait du rôle dynamique de ce Jet dans leur formation, ces dépressions sont appelées dépressions subtropicales. Différentes données montrent que ces dépressions ont joué un grand rôle dans la paléoclimatologie saharienne. En accord avec les botanistes, on définit ainsi une zone climatique particulière du Sahara central.

Diverses études hydrologiques ayant montré qu'en Afrique tropicale un lien direct existe entre le régime des pluies et les caractéristiques de l'écoulement dans les cours d'eau, on peut conclure que le changement hydrologique majeur survenu vers 7 000 ans BP a correspondu à un changement dans le caractère des pluies. On montre que ce changement a résulté d'une modification de la taille des gouttes de pluie. Il apparaît en effet que suivant la taille des gouttes de pluie, l'évolution morphologique du paysage, les caractéristiques hydrologiques des cours d'eau et la granulométrie des sédiments déposés sont différentes. Ainsi on peut conclure qu'entre 15 000 et 7 000 ans BP les pluies fines à gouttes inférieures à 2 mm ont dominé, tandis qu'après 7 000 ans BP environ et jusque vers 4 000 ans BP, ont dominé les pluies à grosses goutes supérieures à 2 mm, engendrées comme actuellement dans les cumulonimbus des dépressions mobiles.

ABSTRACT

LATE QUATERNARY HISTORY OF VEGETATION AND CLIMATE OF TROPICAL NORTH AFRICA

The critical examination of available pollen data from the vegetation of the Sahara allows one to conclude that this vegetation has gone through but few qualitative changes during the last twenty thousand years. In particular, one notices an extension in the Sahara of tropical Sahel taxa about the middle of Holocene. Quantitatively, some pollen and geological data converge to show that the Saharian plains were extremely arid between about 20 000 and 15 000 years BP and that on the mountains the vegetation became very sparse. A new colonization began on the mountains about 15 000 years ago.

The pollen study of Holocene sediments from the central part of the Chad basin was done in the Tjéri station. The results of this study exhibit a major change near 7 000 years BP, characterized in the Sahel zone by a dramatic extension of arboreal taxa until about 5 000 years BP, probably corresponding to northward extension of the sahel savanna. One important change took place also at the same time in the wet north tropical zone where, between about 7 000 and 4 000 years BP, there occurred an extension of taxa growing presently on the well-leached soils of interfluves.

Such a change near 7 000 years BP also appears in the available stratigraphical, sedimentological and pedological data from tropical north Africa. One observes particularly that, between 15 000 and 7 000 years BP, the

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* La présente étude couvre une région qui s'étend essentiellement du Sahara central à la zone soudano-guinéenne (Fig. 1) en excluant la zone de la forêt dense humide. La période étudiée concerne approximativement les 20 derniers millénaires.

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sedimentation was essentially of clay type with a vertisolic pedogenesis (montmorillonite dominant) while, after 7 000 years BP, the sedimentation became coarser, of sandy type, and on the interfluves a pedogenesis of tropical ferruginous type (kaolinite dominant) occurred. It appears that the dramatic change of sedimentation corresponded to a major hydrological change and in particular the deposition of coarser sandy sediments must be associated with flash floods similar to the present-day floods.

The palaeoclimatological interpretation of these data require first a precise knowledge of the present-day dynamic climatology of these regions. So, one must distinguish the rains forming in the monsoon from those which form in the tropical zone farther to the north, particularly in the central Sahara. The latter result from depressions generated by the Subtropical Jet Stream. In these tropical depressions the water vapor precipitated is of equatorial origin. Several data show that these depressions played an important role in the Saharian palaeoclimatology. So, in agreement with the conclusions of botanists, one defines a particular climatic zone across the central part of Sahara.

Several hydrological studies have shown that in tropical Africa there is a direct connection between the rains régime and the characteristics of the river flow. From this fact one can conclude that the major hydrological change of about 7 000 years BP was the result of a change in the character of the rains. One can show that this change resulted from modification in the raindrops size. Indeed, changes in the size of raindrops lead to modifications in the morphological evolution of landscape, in the hydrological characteristics of rivers and in the granulometry of the deposited sediments. So one can conclude that between 15 000 and 7 000 years BP, fine rains with drops smaller than 2 mm dominated whereas, from 7 000 to about 4 000 years BP rains with drops larger than 2 mm, originating, like today, from the cumulonimbus of mobile depressions, were dominant.

1 LE SAHARA CENTRAL

1.1 *Introduction*

Nos connaissances sur la végétation de l'Afrique nord-tropicale au Quarternaire récent sont dues dans leur quasi totalité à la palynologie. Les premières recherches palynologiques au Sahara central (Fig. 1) furent effectuées essentiellement dans la région du Hoggar par Pons & Quezel (1956, 1958) Quezel & Martinez (1958–59,1962), puis par Van Campo *et al.* (1964,1967). Une des principales données qui ressortait des analyses polliniques était la présence, parfois en grande quantité, de pollens provenant de taxons dont l'aire de répartition actuelle ne s'étend pas au Sahara, mais se situe en région tempérée ou (et) en région méditerranéenne.

La possibilité d'un transport par le vent de ces pollens depuis les régions tempérée ou méditterranéenne avait été envisagée dès ces premières études, mais Quézel & Martinez (1959–59) avaient conclu que cela était très improbable, en particulier du fait que dans les sédiments étudiés se trouvaient fréquemment des fragments de bois de quelques millimètres qui ressemblaient beaucoup à des bois de Conifères. Or comme les spectres polliniques comportaient souvent de nombreux pollens de Conifères, cette donnée semblait être effectivement un argument irréfutable. Toutefois, la détermination de ces fragments de bois n'ayant pas été confirmée dans une publication ultérieure (Quézel, *commun.pers.* 1981), on ne doit donc pas exclure la possibilité d'un transport par le vent de ces pollens.

1.2 *La pluie pollinique au Sahara*

Cette question a été étudiée en détails dans le Laboratoire de Palynologie de Montpellier et en 1973, Van Campo publiait les premiers résultats d'une étude sur la pluie pollinique actuelle au Sahara occidental, dans laquelle il ressortait en particulier que les pollens de taxons vivant en région méditerranéenne ou tempérée représentaient environ 20% du spectre au Sahara septentrional à

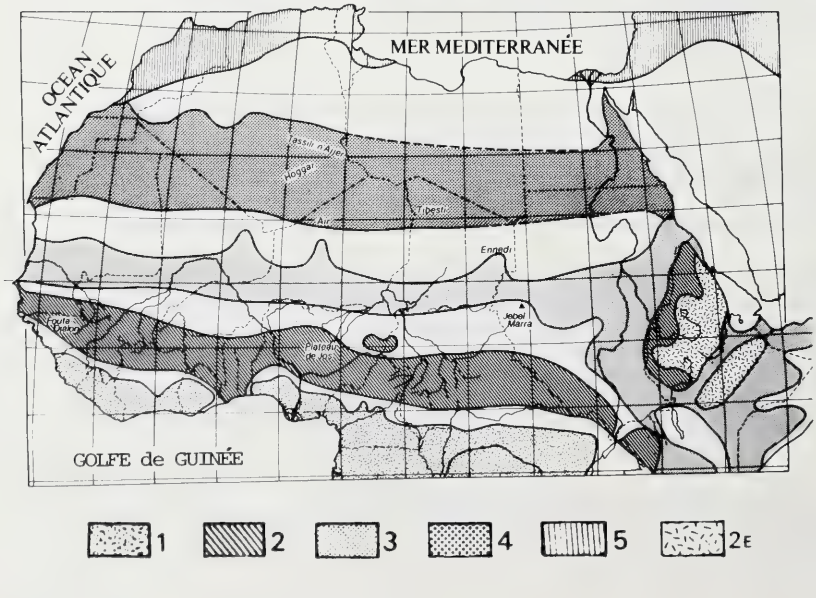

FIG. 1. —Carte schématique des principales zones climatiques et de végétation de l'Afrique au nord de l'équateur. (Sources: entre l'équateur et la zone sahélienne, d'après la carte de végétation de l'AETFAT, 1958; pour le Sahara, les traits pleins sont d'après Quezel, 1965 et les pointillés sont une estimation, Maley, 1981). Pour les figurés, une zone sur deux est représentée en blanc, avec la légende en 'b'. 1, Zone Guinéenne (Forêt Dense Humide); 1b, Zone de transition (Mosaïque Forêt-Savane); 2, Zone Soudano-Guinéenne (2E, Hauts Plateaux Ethiopiens); 2b, Zone Soudanienne; 3, Zone Sahélienne; 3b, Zone du Sahara méridional ou tropical; 4, Zone du Sahara Central; 4b, Zone Saharo-Sindienne; 5, Zone Méditerranéenne.

TABLEAU 1. – Analyses polliniques de sédiments du Tibesti (Actuel et Pléistocène Supérieur)

	Taxons	Petit Trou au Natron Actuel		Diatomites du Trou au Natron (Pléistocène terminal)							
				n° 688 (ca. 17000 BP)		n° 687		n° 689 (14970±400 BP)		n° 690	
		Nb	%	Nb	%	Nb	%	Nb	%	Nb	%
	Gramineae	7	1,5	12	4,4	7	3,9	30	13,9	49	20,0
	Cyperaceae	9	1,9	1	0,4	1	0,5	5	2,3	55	22,5
	Typha							1	0,4	3	1,2
SM	*Artemisia*	57	12,1			8	4,4	3	1,4	16	6,5
SM	cf. *Pentzia monodiana*	27	5,7								
SM	*Erica arborea*					1	0,5	2	0,9	16	6,5
SS	*Ephedra*	105	22,3								
SS	Compositae, tubuliflores	92	19,5			1	0,5			5	2,0
SS	*Launaea*	10	2,1							1	0,4
SS	Cruciferae	28	5,9							1	0,4
SS	Chenopod.-Amaranthaceae	103	21,9							55	22,5
SS	*Euphorbia*	13	2,7							1	0,4
SS	*Rhus*									3	1,2
SS	*Moltkia ciliata*	1	0,2								
SS	*Rumex*	2	0,4								
SS	*Silene*	1	0,2								
T	*Tribulus*	4	0,8								
T	*Maerua crassifolia*	1	0,2							2	0,8
T	*Peristrophe bicalyculata*									1	0,4
T	*Acacia*									1(hors compte)	
M	*Pinus*	2	0,4								
	Ricinus	4	0,8								
				Spores							
	Pteris dentata			182	67,4	39	21,8	75	34,9	3	1,2
	Pteris vittata			1	0,4	3	1,6	1	0,4	1	0,4
	cf. *Cheilanthes*			10	3,7	18	10,0	21	9,7	1	0,4
	Actiniopteris radiata			2	0,7	4	2,2	4	1,8	1	0,4
	Anogramma leptophylla			1	0,4	7	3,9	6	2,8	1	0,4
	Asplenium cf. *aethiopicum*							1	0,4		
	Ophioglossum			2	0,7	21	11,7	6	2,8	2	0,8
	Riccia			1	0,4	5	2,8	1	0,4	2	0,8
	Anthocerotales			3	1,1	13	7,2	14	6,5	5	2,0
	Reboulia			2	0,7						
	Hépatiques					1	0,5			15	6,1
	Spores, type monolète lisse	2	0,4	50	18,5	50	27,9	45	20,9	5	2,0
	Total des spores	2	0,4	254	94,0	161	89,9	174	80,9	36	14,7
	Total autres taxons	466	99,1	13	4,8	18	10,0	41	19,0	208	85,2
	Indéterminés	2	0,4	3	1,1	–		–		–	
	Somme de base	470		270		179		215		244	
	Abîmés	42	8,2	1	0,3	8	4,2	13	5,7	35	12,5
	Total des pollens comptés	512		271		187		228		279	
	SM		17,8		–		4,9		2,3		13,0
	SS		65,2		–		0,5		–		26,9
	T		1,0		–		–		–		1,2
	M		0,4		–		–		–		–

SM, Saharo-Montagnard; SS, Saharo-Sindien; T, Tropical; M, Méditerranéen.

Béni-Abbès (30°N), 9,25% dans la partie la plus aride du Sahara au centre du Tanezrouft (26°N) et environ 1% à la limite sud du Sahara (21°30'N). Ces données ont été complètées ultérieurement (Cour,1974; Cour *et al.*, 1973, 1980) et des résultats comparables ont été aussi obtenus en Libye (Schulz,1979, 1980). Concernant particulièrement les pollens des taxons arborés, les pourcentages au Sahara occidental sont de 5% vers 27°N et de 1% vers 24°N (Cour *et al.*,1980 et *commun. pers.*). D'après les auteurs ci-dessus, la liste suivante peut-être donnée des taxons arborés dont les pollens sont transportés actuellement au Sahara: *Abies, Acer, Alnus,* Betulaceae *Buxus, Carpinus Castanea, Cedrus, Corylus, Fraxinus,* Juglandaceae, *Phillyrea, Platanus, Quercus, Tilia, Ulmus, Vitis.*

Etant donné que les pollens d'origine holarctique observés dans les divers sédiments étudiés se retrouvent dans cette liste, il est donc très possible qu'ils aient été aussi apportés par le vent, d'autant plus que les valeurs des pourcentages des pollens transportés actuellement au Sahara sont certainement très inférieures à ce qu'elles seraient,si les végétations dont ils proviennent étaient peu ou pas altérées par l'homme, particulièrement en ce qui concerne la végétation arborée.

Dans les nombreuses analyses polliniques effectuées au cours de la dernière décade sur des sédiments du Quaternaire récent du Tibesti et du Djado à l'ouest de ce massif (Schulz, 1974, 1979; Maley, 1981), il est apparu que les pollens de taxons holarctiques étaient dans la plupart des analyses totalement ou quasi totalement absents. De ce fait, les forts pourcentages de ces pollens observés par Schulz (1974) dans quelques échantillons du Tibesti apparaissent aberrants et dus certainement à des apports par le vent (Schulz, 1979, 1980).

1.3 *Quelques données palynologiques sur la végétation du Tibesti entre environ 17 000 et 6 600 ans BP*

Grâce à de nombreuses données stratigraphiques et radiochronologiques, le Tibesti est actuellement le massif saharien dont l'évolution géologique au Quarternaire récent est la mieux connue (Fig.2). On présente ici des analyses polliniques effectuées sur des dépôts lacustres prélevés sur les hauts plateaux du Tibesti entre 1 800 et 2 700 m et s'échelonnant entre environ 17 000 ans BP et l'Holocène inférieur (Tableaux 1 et 2), période pour laquelle on possède des échantillons pollénifères (Maley, 1981). Pour comparaison, on présente aussi l'analyse pollinique d'une colluvion actuelle venant de cette région (Tableau 1, colonne 1).

L'étude détaillée de ces spectres ayant déjà été publiée ailleurs (Maley,1981), on ne présente ici que les conclusions principales:

— Malgré la présence d'étendues lacustres importantes au Tibesti entre environ 17 000 ans BP et l'Holocène inférieur — ce qui témoigne de conditions climatiques différentes de l'actuel — la flore pollinique était alors *qualitativement* comparable à celle qui vit actuellement sur les hauts plateaux du Tibesti (Quézel,1958,1965). Cette flore pollinique est composée essentiellement de taxons saharo-montagnards et saharo-sindiens avec aussi un petit nombre de taxons tropicaux, ces derniers étant surtout fréquents sur les flancs de ce massif. Il semble donc qu'au Quaternaire récent la végétation devait être aussi composée essentiellement des éléments saharo-montagnard, saharo-sindien et, dans une moindre mesure, tropical;

— L'importance et la grande variété des spores de Fougères et d'Hépatiques est aussi à noter, alors qu'actuellement leur extension et leur variété sont réduites. Ces plantes devaient probablement vivre surtout à la périphérie des étendues lacustres. Le caractére xérophile de ces Fougères et de ces Hépatiques est à noter. Ce fait est à rapprocher de celui très marqué des taxons saharo-montagnards, saharo-sindiens et tropicaux qui composaient alors l'essentiel de la végétation.

Ces données indiquent clairement qu'une saison sèche annuelle existait à cette époque. On doit donc penser que les extensions lacustres, certaines très importantes (par exemple le lac du Trou au Natron avait une profondeur d'eau de plus de 330 m), peuvent s'expliquer d'abord par une certaine pluviosité annuelle, mais aussi par une réduction de l'évaporation liée à une baisse de la température et probablement à une couverture nuageuse et à des brouillards fréquents (cf.infra et Maley,1981).

La grande rareté des pollens de Phanérogames dans les deux échantillons du Trou au Natron situés entre environ 17 000 et 15 000 ans BP (n°688 et 687) n'est pas due à l'altération des sédiments, car la matière organique est parfaitement conservée. Il est probable que la raréfaction des taxons saharo-montagnards et saharo-sindiens soit dûe à la baisse de la température qui, suivant les auteurs, aurait été de 6° à 10°C (Maley, 1981), et à l'extension de la neige et certains phénomènes périglaciaires sur les hauts plateaux du Tibesti (Messerli,1972). D'autre part, comme les données géologiques le montrent, le climat désertique intense qui règnait à ce moment dans les plaines du Sahara méridional (Fig.2) et du Sahara septentrional (Conrad,1969; Wendorf *et al.*,1976) avait dû aussi raréfier considérablement la végétation de ces régions.

1.4 *Interprétation paléoclimatique: le rôle du 'Jet Stream Subtropical' dans l'évolution climatique du Sahara central*

Afin d'essayer de comprendre comment des précipitations pouvaient affecter alors le Sahara central et surtout les zones montagneuses, tandis que les plaines du nord et du sud du Sahara demeuraient très arides, il est nécessaire de faire appel à un système de pluies particulier qui est lié à l'activité de 'Jet Stream Subtropical'. En effet, l'étude détaillée de la climatologie dynamique de la zone nord-tropicale africaine montre qu'actuellement deux systèmes de pluie d'origine différente peuvent exister au Sahara. Sans entrer dans les détails qu'on trouvera ailleurs (Jalu,1965; Dhonneur,1974; Flohn,1971; Maley,1977,1981) on observe que, d'une part au coeur de l'été, des pluies se forment dans la mousson lorsque celle-ci s'étend sur le Sahara central après avoir envahi toute la zone nord tropicale africaine. D'autre part, on observe

TABLEAU 2. – Analyses polliniques de sédiments du Tibesti (Holocène inférieur)

	Taxons	Emi Koussi n° 1 (Holo.inf.?)		Mouskorbé n° 10 (8530 ± 100)		Mouskorbé n° 9 (6700 ± 140)		Mouskorbé n° 3 (6600 ± 140)		Tarso Yéga n° 5 (7100–6600?)	
		Nb	%	Nb	%	Nb	%	Nb	%	Nb	%
	Gramineae	233	24,7	69	12,6	12	4,2	90	25,5	10	3,2
	Cyperaceae	47	5,0	16	2,9	4	1,4	35	9,9		
	Typha	1	0,1			1	0,3	6	1,7		
SM	*Artemisia*	462	49,0	76	13,9	90	31,8	75	21,2	198	63,0
SM	cf*Pentzia monodiana*	14	1,5	32	5,8	27	9,5	11	3,1	13	4,1
SM	*Erica arborea*	1	0,1								
SM	*Galium*	4	0,4								
SS	*Ephedra*			3	0,5	27	9,5	3	0,8	8	2,5
SS	Compositae, tubuliflores	5	0,5	94	17,2	11	3,9	4	1,1	9	2,8
SS	Chenopod.-Amaranth.	4	0,4	143	26,2	48	17,0	2	0,5		
SS	Cruciferae	28	2,9	8	1,4	7	2,4	6	1,7		
SS	*Launaea*	1	0,1	6	1,1	6	2,1				
SS	*Plantago*			8	1,4	4	1,4				
SS	*Zygophyllum*			4	0,7	17	6,0			59	18,8
SS	*Fagonia*			1	0,2	3	1,0				
SS	*Euphorbia*	4	0,4	17	3,1	7	2,4	2	0,5	6	1,9
SS	*Erodium*	12	1,2	3	0,5			7	2,0		
SS	*Aizoon canariense*	24	2,5								
SS	*Phoenix*							3	0,8		
SS	*Silene*	8	0,8					1	0,3		
SS	*Heliotropium*	1	0,1	1	0,2						
SS	Urticaceae	1	0,1	3	0,5						
SS	*Moltkia ciliata*					1	0,3				
SS	Asclepiadaceae					1	0,3				
SS	Papilionaceae	1	0,1							2	0,6
SS	*Rhus*	3	0,3			1	0,3				
SS	*Androcymbium*	1	0,1								
T	*Tribulus*	1	0,1	9	1,6	3	1,0				
T	*Indigofera*	1	0,1								
T	*Aerva persica*			2	0,3	1	0,3				
T	*Chrozophora*			1	0,2						
T	*Acacia* (Gummiferae)					1	0,3				
T	Combretaceae	1	0,1								
	Haloragaceae	49	5,2								
M	*Pinus*					1	0,3				
	Spores										
	Pteris dentata							10	2,8		
	Pteris vittata							4	1,1		
	cf. *Cheilanthes*			1	0,2			10	2,8		
	Actiniopteris radiata	1	0,1	1	0,2			4	1,1		
	Anogramma leptophylla	4	0,4					1	0,3		
	Ophioglossum	2	0,2	12	2,2			12	3,4	5	1,6
	Riccia	1	0,1	4	0,7			14	3,9	1	0,3
	Anthocerotales	9	0,9	24	4,4	4	1,4	13	3,7	1	0,3
	Hépatiques			5	0,9						
	Spores, type monolète lisse	17	1,8					38	10,7	2	0,6
	Total des spores	34	3,6	47	8,6	4	1,4	106	30,0	9	2,8
	Total autres taxons	907	96,3	496	91,0	273	96,4	245	69,4	305	97,1
	Indéterminés	1	0,1	2	0,3	6	2,1	2	0,5		
	Somme de base	942		545		283		353		314	
	Abîmés	50	5,0	76	12,2	55	16,2	56	13,7	45	12,5
	Total pollens comptés	992		621		338		409		359	
	SM	52,2		19,8		41,3		24,3		67,1	
	SS	8,3		53,3		46,7		7,9		26,6	
	T	0,3		2,2		1,7		–		–	
	M	–		–		0,3		–		–	

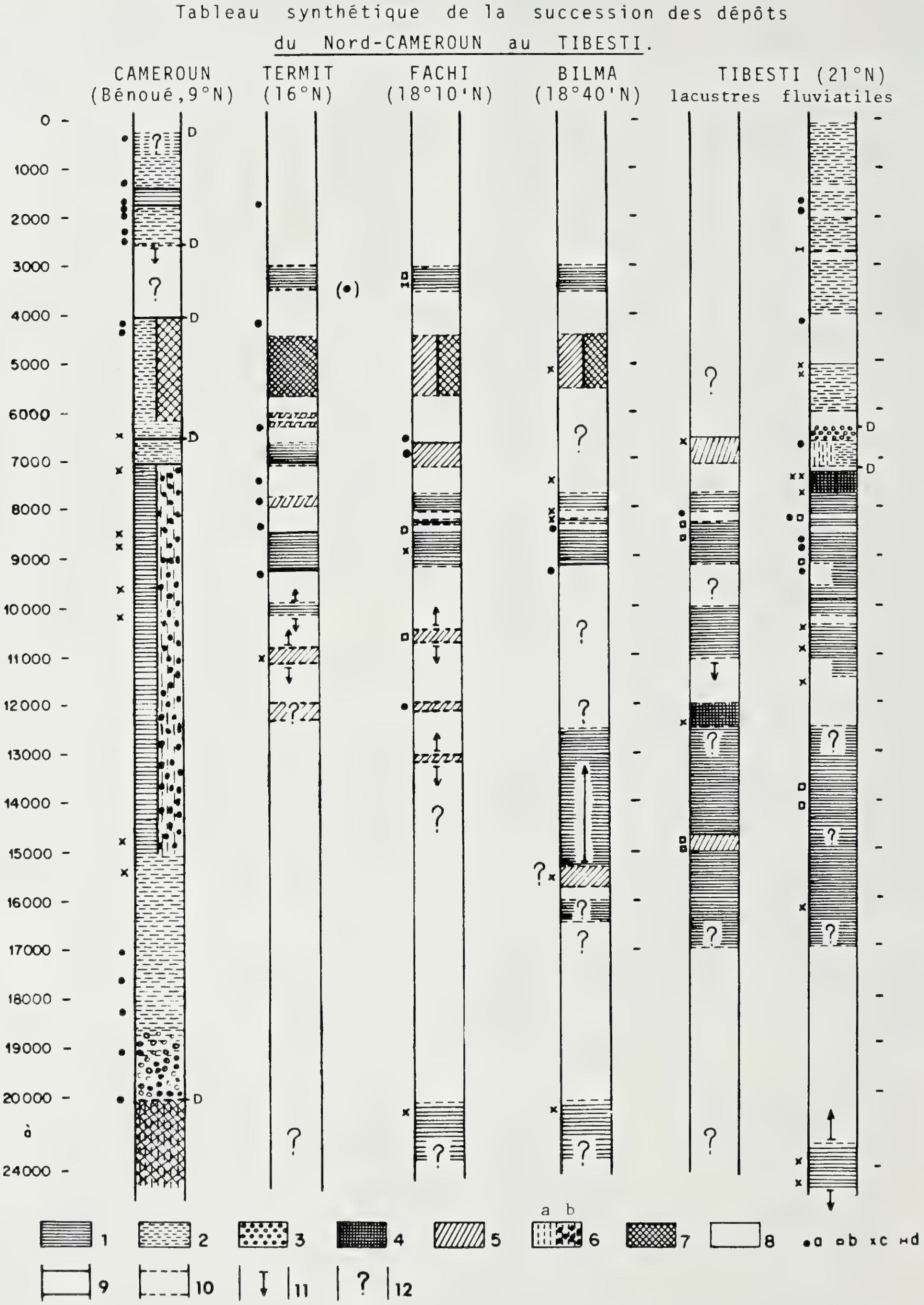

FIG. 2.—Tableau synthétique de la succession des dépôts sédimentaires à la longitude du Bassin du Tchad entre la zone tropicale humide et le Sahara Central pour des lacs ou rivières ayant de relativement petits bassins versant couvrant seulement une zone climatique. 1, Extension lacustre ou dépôts fluviatiles relativement fins et lités. 2, Sables et cailloutis; 3, Galets; 4, Croûte calcaire; 5, Lac réduit ou marécage; 6a, Paléosols divers; 6b, Vertisols; 7, Cuirasse ferrugineuse ou paléosol de type ferrugineux tropical; 8, Période aride (sables éoliens, etc); 9, Limites relativement bien datées; 10, Limites estimées; 11, Déplacement possible d'une limite chronologique; 12, Données ou périodes à préciser. D, Discontinuité. Position des *datations C–14* et nature des échantillons datés: a, sur charbon ou débris végétaux; b, sur coquilles; c, sur calcaire; d, sur os. ( ), datation importante dans un site voisin. Maley (1981) pour les références aux données stratigraphiques de base. *Note :* Les dépôts lacustres de Bilma de la fin du Pléistocène, si leur position chronologique est confirmée, résulteraient probablement d'apports artésiens en provenance du Sahara central (extrait de Maley, 1981).

qu'il y a aussi parfois formation de pluies durant les autres saisons de l'année, alors que le front de la mousson se situe très loin au sud du Sahara. D'un point de vue synoptique, ce second type de pluie se produit, en bref, lorsqu'une coulée d'air polaire s'avance en altitude vers le sud dans une ondulation du 'Jet Subtropical' qui, de l'automne au printemps, circule régulièrement d'ouest en est au-dessus du Sahara. Le système dépressionnaire qui se forme dans la moyenne troposphère à l'avant de l'ondulation du 'Jet', détruit localement et provisoirement l'anticyclone saharien et, en même temps, provoque ou favorise quelquefois de brèves expulsions vers le nord d'air équatorial humide (il ne s'agit pas alors de mousson). L'examen de photos de satellite montre que ces masses d'air humide viennent fréquemment de différents secteurs du Golfe de Guinée et parfois de plus à l'est (Morel *et al.*1978). Le mélange de l'air polaire d'altitude, toujours très sec, avec l'air humide équatorial, entraîne très rapidement la formation de nuages qui, emportés par le courant directeur du 'Jet' (Fig.3), suivent une trajectoire d'allure parabollique et sont entraînés finalement vers l'est en déversant leurs pluies à travers le Sahara. Actuellement le parcours du Jet coupe parfois transversalement le Sahara et dans ce cas la dépression pluvieuse (ou sèche si elle n'a pas été alimentée en air humide) s'éloigne en direction de la Méditerranée ou du Moyen-Orient.

L'importance pour la paléoclimatologie saharienne des pluies liées à ces dépressions a été déjà postulée par Dubief (1963) puis par Maley (1977,1981) et Nicholson & Flohn (1980). Une donnée intéressante en ce sens ressort d'une étude isotopique des eaux fossiles du Quaternaire récent d'une partie du Sahara libyen (Edmunds *et al.*,1979). Ces auteurs (ibid.) ont montré que bien que les pluies étaient alors froides, la vapeur d'eau précipitée était d'origine équatoriale. Cette constatation s'explique très bien par ces dépressions pluvieuses qui résultent d'un mélange d'air polaire et d'air humide équatorial. On doit remarquer que seules apparemment les zones montagneuses ont bénéficié de ces pluies entre environ 17 000 ans et le début de l'Holocène. A part les parties basses à la périphérie des montagnes qui pouvaient recevoir des éculements fluviatiles ou phréatiques ou éventuellement artésiens, l'absence de traces d'humidité dans les plaines du Sahara central pourrait s'expliquer par la violence des vents de sable à cette époque.

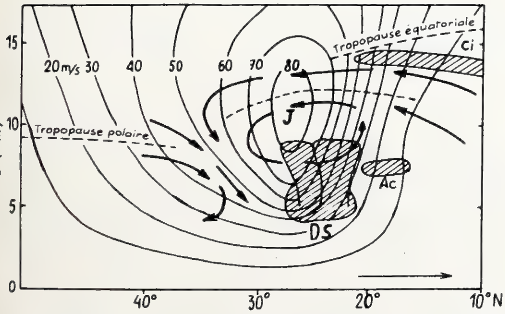

FIG. 3.—Coupe transversale du Jet Subtropicale durant la saison fraîche; position d'une dépression subtropicale (DS); Ac, Altocumulus; Ci, Cirrus. Les flèches indiquent la circulation transversale au Jet avec développement de subsidence ou de convergence dynamique de part et d'autre de l'axe du Jet (adapté d'après Queney, 1974 et autres sources; Maley, 1981).

Actuellement, bien que les pluies liées aux dépressions tropicales soient généralement faibles, elles constituent cependant souvent un pourcentage important du total des pluies (Dubief, 1963; Maley, 1981). Ainsi il apparaît que, tout au long de la saison fraîche, d'Octobre à Mai, le 'Jet Stream Subtropical' alors dans sa position latitudinale la plus basse, exerce à long terme un rôle climatique indéniable. Au Quaternaire récent ce rôle s'est manifesté par la formation de la 'Moyenne Terrasse', dépôt fluviatile typique du Sahara central, ainsi que par les formations lacustres contemporaines, qui ont été datées entre environ 17 000 et 6 500 ans BP (Fig.2) (Maley, 1977,1981). Par contre, à l'Holocène moyen, l'érosion de cette terrasse et les sédiments grossiers qui se sont alors déposés dans les vallées (Fig.2), témoignent d'un climat différent (Maley, 1977, 1981). D'après ces données et d'autres exposées brièvement plus bas, il apparaît que les pluies de mousson ont dû alors s'étendre en été au Sahara central en prenant les pas sur les pluies des dépressions tropicales.

Il est donc ainsi possible de définir une zone climatique particulière du Sahara central où alternent et s'interpénètrent au cours du temps, et durant certaines périodes annuellement, des pluies estivales de mousson et des pluies de saison fraîche liées à l'activité du 'Jet Stream Subtropical'. Cette conclusion rejoint les conceptions botaniques de Monod (1944) et en particulier de Quézel (1965) qui a défini une zone de végétation du Sahara central dans laquelle s'interpénètrent des espèces de souche africaine et d'autres de souche mésogéenne ou méditerranéenne. La persistance de plantes reliques sur les montagnes du Sahara (Quézel, 1978; Maley 1980) s'expliquerait par la possibilité particulière de ces montagnes de recevoir des pluies aussi bien durant une phase glaciaire que durant un optimum thermique postglaciaire.

Les données polliniques exposées ci-dessus ainsi que d'autres données présentées plus bas à la fin du paragraphe 2.2, concernant l'extension sur le Sahara à l'Holocène moyen d'un élément tropical de type sahélien, ainsi que des sols ferrugineux tropicaux, ne permettent pas de retenir l'hypothèse avancée précédemment (Quézel & Martinez, 1958-59, carte 2) d'une migration à l'Holocène de taxons méditerranéens sur les montagnes du Sahara central. Hypothétiquement, une telle migration aurait pu se produire entre 30 000 et 40 000 ans ou à d'autres périodes plus anciennes. L'étude palynologique de sédiments lacustres du Sahara septentrional et central situés entre 20 000 et 40 000 ans et plus anciens, serait nécessaire pour pouvoir conclure précisément à ce propos.

TABLEAU 3. – Taxons caractéristiques des pollens déterminés sur la coupe de Tjéri. Classement par Eléments et groupes écologiques

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Elements et groupes ecologiques
Taxons

Elément SAHELIEN

Amaranthaceae (type)
Acacia, Gummiferae (Mimosaceae)
Acacia raddiana (Mimosaceae)
Acacia cf. *A. senegal* (Mimosaceae)
Acacia seyal (Mimosaceae)
Balanites aegyptiaca (Balanitaceae)
Borreria sp. (Rubiaceae)
Capparis decidua (Capparaceae)
Capparis sp. (Capparaceae)
Celosia trigyna (Amaranthaceae)
Cocculus pendulus (Menispermaceae)
Commiphora africana (Burseraceae)
Compositae, Tubuliflores
Hyphaene thebaica (Palmae)
Indigofera sp. (Papilionaceae)
Maerua crassifolia (Capparaceae)
Mitracarpus scaber (Rubiaceae)
Monechma ciliata (Acanthaceae)
Oldenlandia sp. (Rubiaceae)
Salvadora persica (Salvadoraceae)
Trianthema pentandra (Aïzoaceae)
Tribulus sp. (Zygophyllaceae)

Elément SOUDANIEN

Allophyllus africanus (Sapindaceae)
Celtis integrifolia (Ulmaceae)
Clematis hirsuta (Ranunculaceae)
Combretaceae
Dombeya quinqueseta (Sterculiaceae)
Lannea sp. (Anacardiaceae)
Mitragyna inermis (Rubiaceae)
Morelia senegalensis (Rubiaceae)
Prosopis africana (Mimosaceae)

Elément SOUDANO-GUINEEN

Adina sp. (Rubiaceae)
Alchornea cordifolia (Euphorbiaceae)
Bridelia ferrugina (Euphorbiaceae)
Bridelia cf. *B. scleroneura* (Euphorbiac.)
Elaeis guineensis (Palmae)
Hymenocardia acida (Euphorbiaceae)
Nauclea sp. (Rubiaceae)
Olea hochstetteri (Oleaceae)
Uapaca sp. (Euphorbiaceae)

Elément MONTAGNARD (Tibesti)

Artemisia sp. (Compositae)
Ephedra sp. (Ephedraceae)
Erica arborea (Ericaceae)
Pentzia monodiana (Compositae)
Plantago (Plantaginaceae)
Silene sp. (Caryophyllaceae)

Groupe des Plantes HYGROPHILES

Cissus ibuensis (Vitaceae)
Hygrophila sp. (Acanthaceae)
Ipomoea sp. (Convolvulaceae)
Laurembergia tetrandra (Haloragaceae)
Ludwigia sp. (Onagraceae)
Nymphaea sp. (Nymphaeaceae)
Polygonum sp. (Polygonaceae)
Sesbania pachycarpa (Papilionaceae)

Spores

Azolla africana (Azollaceae)
Ceratopteris cornuta (Adiantaceae)
Ophioglossum sp. (Ophioglossaceae)
Spore monolète

2 LA ZONE SAHELIENNE

2.1 *Le Pléistocène terminal*

La grande phase aride de la fin du Pléistocène supérieur a affecté aussi la zone sahélienne (Fig.2) et ce n'est que vers 13 000 ans BP que quelques dépôts lacustres très limités réapparaissent au Tchad. Au Kanem, au NE du lac actuel, l'étude des diatomées (Servant-Vildary, 1978) a montré le caractère saumâtre de ces étendues lacustres qui étaient alimentées en grande partie par la nappe phréatique et par des apports fluviatiles allochtones venant de la zone tropicale humide (Fig.2 et Maley, 1981). L'étude des pollens montre une apparition timide de la végétation sahélienne entre environ 13 000 et 12 500 ans BP. L'amélioration climatique s'est poursuivie ensuite entrecoupée de phases arides (Fig.2). C'est apparemment seulement vers 10 100 ans BP qu'ont pu exister brièvement dans des petits bassins isolés de la zone sahélienne des lacs alimentés essentiellement par les pluies régionales (Fig.2 et Maley, 1981). La végétation sahélienne a pris durant cette courte période une première extension comparable à ce qu'elle sera ensuite à l'Holocène inférieur. Une phase aride relativement importante centrée vers 9 700 – 9 500 ans BP se situe au tout début de l'Holocène avant la transgression lacustre de l'Holocène inférieur datée approximativement de 9 200 à 8 500 ans BP.

2.2 *L'Holocène*

L'évolution de la végétation au cours de l'Holocène a été étudiée sur la coupe de Tjéri située au Kanem vers le centre du Paléotchad (Servant, 1973; Maley, 1981). Seuls les principaux résultats sont présentés ici, l'étude palynologique détaillée de cette coupe ayant été publiée récemment par ailleurs (Maley, 1981). Les pollens observés dans les 46 échantillons étudiés ont été classés suivant l'appartenance écologique des taxons dont il sont issus et aussi d'aprés la dominance actuelle plus ou moins marqée de ces taxons dans les différentes zones climatiques du bassin du Tchad (Tableau 3). Les principaux résultats sont synthétisés sur les Figs 4 & 5.

L'étude des diatomées, effectuée sur les mêmes échantillons que ceux utilisés par la palynologie, a permis à Servant-Vildary (1978) de tracer une courbe de la variation de la profondeur de l'eau à la station de Tjéri (Fig.5, courbe a). Vu la position de cette station, cette courbe retrace l'évolution des niveaux du Paléotchad durant l'Holocène. Il apparaît aussi que les principales phases d'extension lacustre mises en évidence grâce à la géologie en divers points de la zone du Paléotchad (Servant, 1973; Maley, 1981), se retrouvent sur cette courbe. Cette concordance est importante car elle permet en particulier de préciser la chronologie de la coupe de Tjéri (Fig.5d). De cette manière on voit que la phase du Paléotchad maximum ou Mégatchad (cordons lacustres vers 320 m), que diverses données situent à l'Holocène moyen (Servant 1973; Maley, 1981), correspond à l'extension maximum de cette courbe (Fig.5a). Il est ainsi possible de corréler la diminution majeure des pourcentages des pollens de l'élément sahélien (Fig.5, courbe c, phase lll) à la grande phase aride située vers 7 500 ans BP. Cette phase aride, bien mise en évidence par des données géologiques (Servant, 1973), a affecté surtout la zone sahélienne ainsi que le Sahara méridional et central (Fig.2). On doit donc conclure que la transgression mise en évidence par les diatomées durant la phase III, n'a pu être causée que par des apports fluviatiles allochtones à la zone tropicale sèche. L'examen des données palynologiques et le fait bien établi que les fleuves du bassin du Tchad transportent des pollens depuis leurs zones d'alimentation (Maley, 1972, 1981), montrent que ces apports fluviatiles venaient de la zone tropicale humide. En effet, dans le contexte climatique de cette époque, le maximum atteint durant la phase III par les pollens de l'élément soudano-guinéen (Fig.5, courbe b), signifie que les apports fluviatiles allochtones alimentant le Paléotchad venaient de la zone tropicale humide qui s'étend sur le sud du bassin du Tchad, où les fleuves Chari et Logone prennent leur source. Des données purement physiques concernant le bassin adjacent du Niger dont les sources (Bénoué et haut Niger) se trouvent essentiellement en zone tropicale humide, indiquent que les apports fluviatiles dans le Golfe de Guinée ont été aussi maximum entre 8 500 et 7 000 ans BP (Pastouret *et al.*, 1978). Un tel déphasage climatique n'est pas un phénomène isolé car d'autres déphasages comparables ont pu être mis en évidence à d'autres époques comme vers le milieu du ler millénaire AD et au 17è s.AD (Maley, 1981).

Concernant l'évolution de la végétation en zone sahélienne, les données polliniques de Tjéri montrent en particulier que les taxons arborés ont dominé à l'Holocène moyen. Cette extension de la végétation de la végétation arborée peut-être associée, d'une part au maximum survenu à cette époque des pollens de l'élément soudanien (Fig.4) qui est composé surtout de taxons arborés (Tableau 3), et d'autre part à l'extension sur le Sahara méridional des sols de type ferrugineux tropical, avec parfois formation de cuirasses ferrugineuses (Fig.2). Ces diverses données semblent indiquer qu'il y a eu à l'Holocène moyen un certain glissement vers le nord des zones climatiques, accompagné probablement d'une certaine extension de l'élément tropical sahélien sur le Sahara méridional et central (cf. supra, fin I,4) Maley, 1977,1981)

3 LA ZONE TROPICALE HUMIDE

3.1 *Quelques données polliniques d'âge holocène*

On ne possède pas actuellement pour cette zone de données polliniques obtenues in situ. Toutefois, quelques données indirectes sont obtenues par les pollens apportés par les fleuves qui se jetaient dans le Paléotchad. A ce propos, il est intéressant de remarquer que les pollens qui sont transportés actuellement dans le lac Tchad depuis la zone soudano-guinéenne (Maley, 1972,1981), sont les mêmes que ceux qui se sont déposés dans les sédiments de Tjéri au cours de l'Holocène (Tableau 3). Cela tendrait à prouver que durant cette période

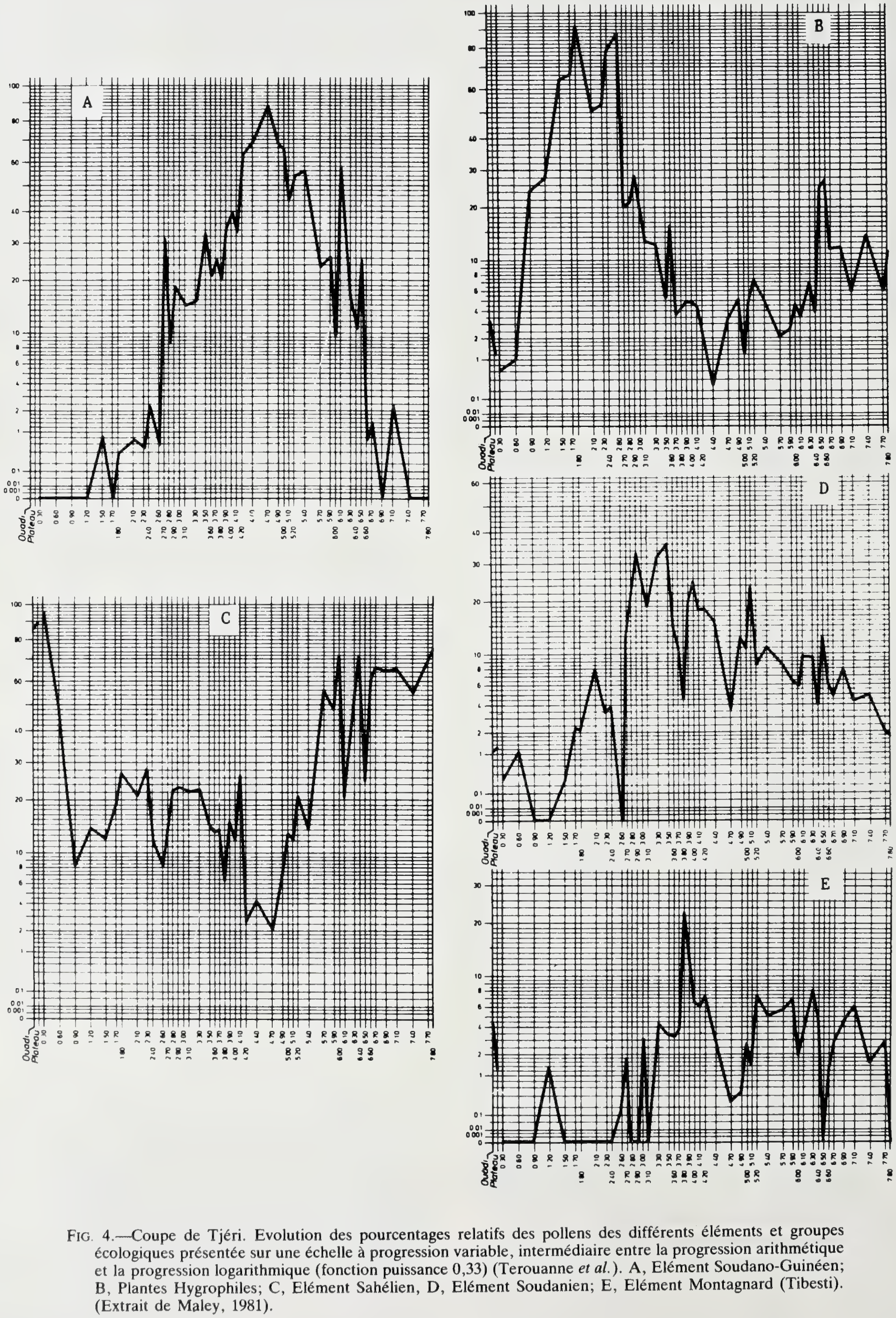

FIG. 4.—Coupe de Tjéri. Evolution des pourcentages relatifs des pollens des différents éléments et groupes écologiques présentée sur une échelle à progression variable, intermédiaire entre la progression arithmétique et la progression logarithmique (fonction puissance 0,33) (Terouanne *et al.*). A, Elément Soudano-Guinéen; B, Plantes Hygrophiles; C, Elément Sahélien, D, Elément Soudanien; E, Elément Montagnard (Tibesti). (Extrait de Maley, 1981).

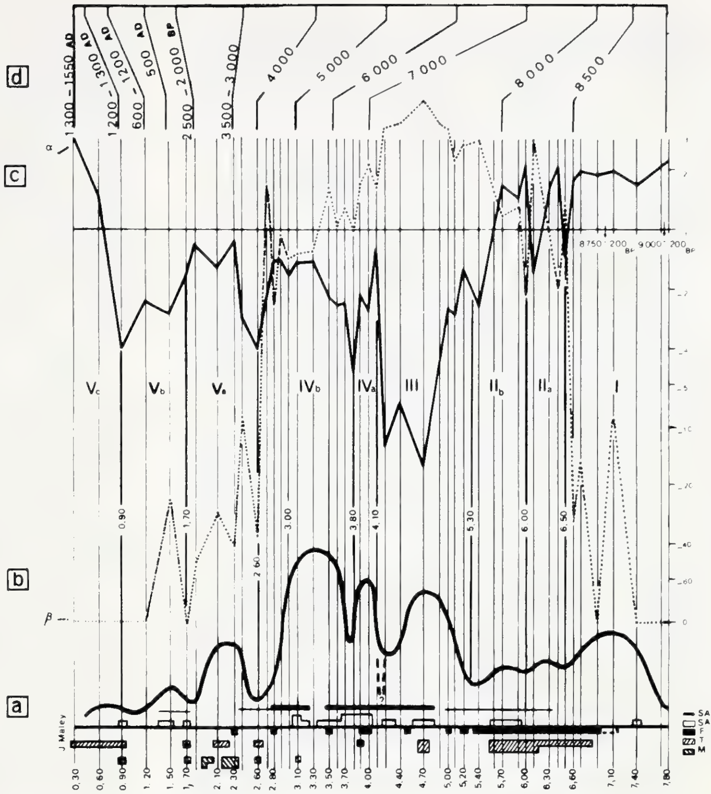

FIG. 5.—Evolution comparée pour la coupe de Tjéri, de bas en haut (extrait de Maley, 1981): a, Niveaux lacustres relatifs d'après les diatomées (Servant-Vildary, 1978); quelques diatomées écologiquement importantes : SA, *Stephanodiscus astrea*; SAm, *Stephanodiscus astrea* var. *minutula*; F, diverses diatomées psychrophiles, surtout *Cymatopleura elliptica* et *Melosira italica* var. *valida;* T, *Cyclotella ocellata;* M, *Melosira italica.* b, Courbe pollinique de l'élément soudano-guinéen (en pointillés), ß pourcentages actuels. c, Courbe pollinique de l'élément sahélien (trait plein), α pourcentages actuels. Les deux courbes b et c ont été construites en utilisant le rapport à la moyenne (valeur 1) sur une échelle logarithmique. d, Chronologie partiellement reconstituée d'après diverses corrélations régionales. Vers la base deux datations au radiocarbone.

et par rapport à l'actuel, il n'y a pas eu de changements qualitatifs marqués de la végétation dans la partie méridionale du bassin. Concernant les pollens déterminés jusqu'à l'espèce, on peut cependant noter que ceux d'*Alchornea cordifolia,* qui se développe surtout sur les sols hydromorphes du fond des vallées, ont dominé durant l'Holocène inférieur, tandis que le pollens d'*Hymenocardia acida* qui se développe surtout sur les sols bien drainés des interfluves, ont nettement dominé à l'Holocène moyen jusque vers 4 000 ans BP.

3.2 *Données pédologiques et géologiques*

Il est certain que ces données polliniques préliminaires devront être précisées et confirmées par des recherches palynologiques effectuées dans le sud du bassin du Tchad ou à son voisinage. Il faut toutefois remarquer que des données venant d'autres disciplines convergent tout à fait avec ces données polliniques. En effet, il apparaît que sur la zone tropicale humide, non seulement vers le sud du bassin du Tchad (Fig.2), mais aussi plus à l'ouest sur l'Afrique occidentale, le Pléistocène terminal à partir d'environ 15 000 ans BP et l'Holocène inférieur jusque vers 7 000 ans BP, ont été caractérisés par l'extension de sols hydromorphes de type vertisolique avec développement de montmorillonite et formation de nodules calcaires. Il faut noter que ces sols nécessitent une certaine saison sèche annuelle. Ensuite, à l'Holocène moyen, entre environ 7 000 et 4 000 ans BP, ces régions ont vu l'extension de sols de types ferrugineux tropicaux qui se développent sur les substrats sableux et bien drainés des interfluves avec formation de kaolinite. Ces types de sol nécessitent aussi une saison sèche annuelle (pour ces divers sols et les néoformations argileuses associées, (cf. Bocquier *et al.*, 1970; Bocquier, 1973; Millot, 1978).

Par ailleurs des données géologiques et sédimentologiques obtenues pour les grands bassins de la zone nord-tropicale africaine (Nil Bleu, Tchad, Bénoué-Niger, Sénégal), montrent que, corrélativement à la formation des sols de type vertisolique entre 15 000 et 7 000 ans BP environ, les fleuves transportaient et déposaient essentiellement des matériaux très fins de type argileux, dont une grande partie était d'origine éolienne (Maley, 1981), tandis qu'entre 7 000 et 4 000 ans BP environ, associée à une nette reprise de l'érosion, la charge alluviale devint plus grossière avec des dépôts de type sableux (Maley, 1981).Ainsi on peut conclure qu'entre 15 000 et 7 000 ans BP environ les cours d'eau étaient lents, à débit régulier et avec de nombreux méandres, tandis qu'entre 7 000 et 4 000 ans BP environ, les crues devinrent très brutales, comme on l'observe actuellement. Durant cette seconde phase, le tracé des flueves se modifia pour devenir plus rectiligne, comme le sont par exemple les chenaux sableux remontant à cette époque qui ont été observés dans la plaine d'inondation du Tchad.

3.3 *Interprétation paléoclimatique*

La conclusion principale qui ressort de ces données est qu'un changement hydrologique majeur est survenu vers 7 000 ans BP. Ce changement est à lier directement à un changement dans le régime des pluies car diverses études hydrologiques conduites sur la zone nord tropicale africaine (Rodier, 1964) ont bien montré le lien direct qui existe entre le régime des pluies et les caractéristiques de l'écoulement dans les cours d'eau.

Lorsqu'on étudie le régime actuel des pluies sur ces régions, on doit noter en particulier qu'il y a deux types principaux de pluie suivant leur position dans la mousson (Dhonneur, 1974).

— A l'avant du front de la mousson se trouve ce que les météorologistes appellent la *zone C1* et qui est caractérisée par le passage de *dépressions mobiles* ou lignes de grains formés par d'épais *cumulonimbus*. L'ensoleillement et l'evaporation sont importants entre le passage des dépressions mobiles.

— A l'arrière de cette zone se trouve la *zone C2* qui est caractérisée par des *dépressions quasi-stationnaires* constituées de *nuages de type stratiforme*. L'évaporation est réduite du fait de l'importance de la nébulosité.

Par ailleurs, étant donné que la taille des gouttes de pluie dépend surtout de la profondeur des nuages (Mason, 1971), les gouttes qui viennent des cumulonimbus ont en grande majorité des diamètres supérieurs à 2 mm, tandis que celles qui viennent des nuages stratiformes ont des diamètres essentiellement inférieurs à 2 mm (Wexler, 1954; Barat, 1957).

Ces distinctions sont très importantes car Barat (1957) a montré dans ses recherches sur la pluie en Afrique tropicale et à Madagascar, que l'érosion des sols est très différente suivant la taille des gouttes de pluie (Fig.6). Les pluies des dépressions quasi-stationnaires (pluies homogènes de Barat), dont les gouttes sont en majorité inférieures à 2 mm, s'infiltrent instantanément ou avec seulement un faible ruissellement pelliculaire sans érosion notable. Les études de Hurault (1975) conduites dans l'Adamaoua, montrent que ce ruissellement pelliculaire conduit à la formation de sédiments fins dans les cours d'eau. Par ailleurs, du fait du volume et du poids relativement importants de la majorité des gouttes de pluie des dépressions mobiles (pluies hétérogènes de Barat), le ruissellement violent qui en résulte conduit à une forte érosion des sols. Dans les cours d'eau il en résulte des dépôts de sédiments grossiers de type sableux (Hurault, 1975). Ainsi on peut conclure, en bref,

— que le dépôt des alluvions argileuses et le développement des sols de type vertisolique entre 15 000 et 7 000 ans BP environ, ont été dûs à une grande extension des pluies fines et des nuages stratiformes, au détriment des pluies à grosses gouttes et des cumulonimbus. L'importance de la poussière saharienne poussée par le vent sur la zone nord-tropicale a dû jouer un grand rôle à cette époque dans l'extension des pluies fines et des sédiments fins (Maley, 1981, 1982)

— que, par contre, après 7 000 et jusque vers 4 000 ans BP, le dépôt de sédiments plus grossiers et la formation des sols ferrugineux tropicaux ont été dûs

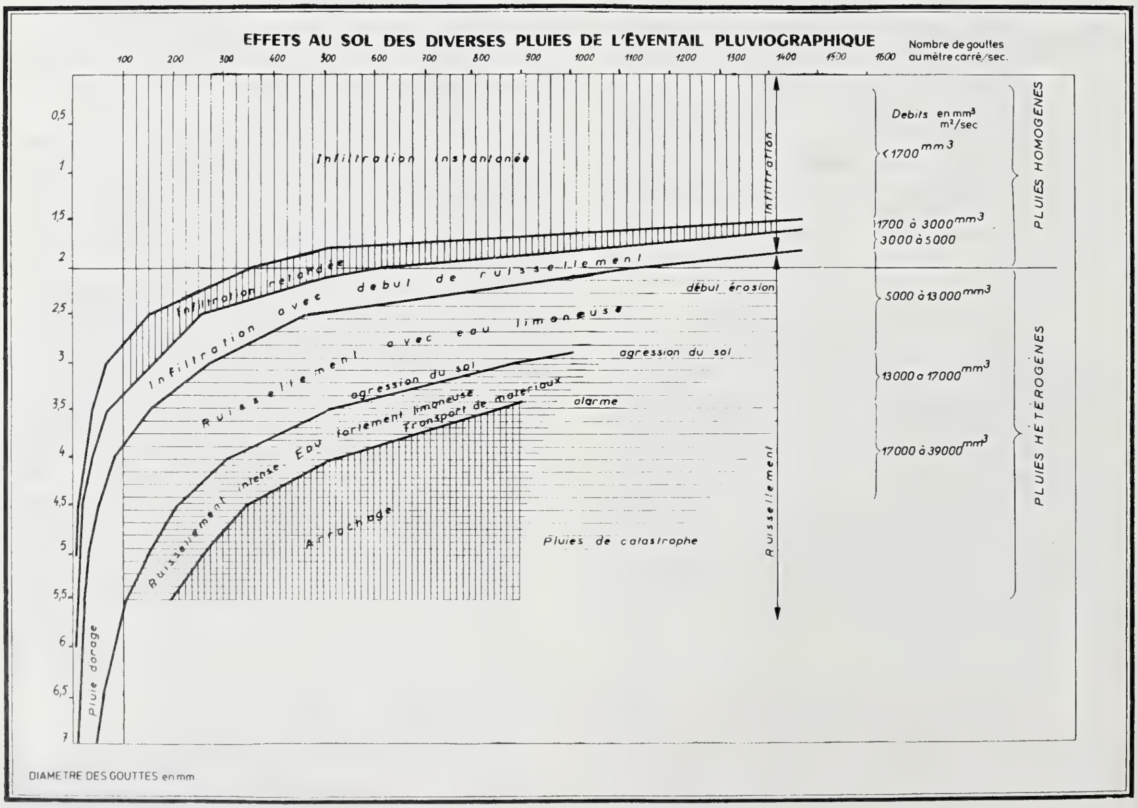

FIG. 6. — Effets au sol des diverses pluies de l'éventail pluviographique (Extrait De Barat, 1957).

à la brutale réapparition et domination des pluies à grosses gouttes des cumulonimbus.

Ainsi, sans changement notable de la longueur de la saison des pluies, il apparaît que des modifications des caractéristiques de la pluviosité et particulièrement des types de nuages, résultant de l'extension de la zone C2 au détriment de la zone C1 ou vice versa, sont capables de provoquer des changements majeurs en hydrologie, sédimentologie, pédologie, géomorphologie et finalement dans la végétation (cette hypothèse est exposée plus en détails dans Maley, 1981,1982).

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Isotopic evidence for the past climates and vegetation of southern Africa

J. C. VOGEL*

ABSTRACT

The stable isotopes of hydrogen, oxygen and carbon can potentially provide evidence of past climates. The most detailed information has been obtained from variations in the oxygen-18 content of foraminifera from ocean floor cores, the analysis of which has produced a record of ocean temperature changes through the Quaternary and beyond. The use of isotope analysis of continental materials to reveal climatic change is more limited, but some advances have been made in recent years.

One approach has been to utilize the variations in the isotopic composition of precipitation as recorded in ancient groundwater. Thus groundwater samples from a confined aquifer on the southern Cape coast show a marked rise in temperature since the Last Glacial maximum. The temperature changes during the Upper Pleistocene and Holocene are also reflected in the oxygen-18 content of stalagmites from the Cango caves in the same region.

The widespread occurrence of C_4 grasses in the warmer summer rainfall areas of southern Africa provides a novel possibility of observing temporal shifts of climatic boundaries. The distinctly high carbon-13 content of C_4 plants is clearly reflected in the skeletons of grazers so that faunal material from suitably situated archaeological sites can be used to observe changes in the composition of the local grass-cover. The evidence thus far accumulated suggests only minor changes since the Upper Pleistocene.

The combined evidence to date indicates that temperatures and also precipitation in southern Africa have changed since the Last Glacial maximum, about 18 000 years ago, but that shifts in the boundaries of the various veld-types were probably not very extensive.

RÉSUMÉ

ESTIMATION AU MOYEN DES ISOTOPES DES CLIMATS ET DE LA VÉGÉTATION DU PASSÉ DE L'AFRIQUE DU SUD

Les isotopes stables d'hydrogène, d'oxygène et de carbone sont à même de nous renseigner sur les climats du passé. Les informations les plus détaillées ont été obtenues à partir de variations de la teneur d'oxygène-18 de foraminifères en provenance de carottes prélevées dans les fonds océaniques, dont l'analyse a fourni une indication sur les changements de température au cours du Quaternaire et auparavant. L'utilisation de l'analyse des isotopes pour des matériaux continentaux en vue de connaître les changements climatiques est plus limitée mais certains progrès ont été réalisés durant ces dernières années.

Une des méthodes a consisté à utiliser les variations de la composition en isotopes des précipitations prélevées dans d'anciennes nappes phréatiques. C'est ainsi que des échantillons de la nappe phréatique d'une couche aquifère retenue en inclusion sur la côte sud du Cap indiquent une nette élévation de la température depuis l'apogée de la dernière période glaciaire. Les changements de température pendant l'Holocène et le Pleistocène supérieur se reflètent aussi dans la teneur en oxygène-18 des stalagmites des grottes de Cango situées dans la même région.

La vaste distribution des graminées à C_4 *dans les régions chaudes à pluies estivales de l'Afrique du Sud fournit une nouvelle possibilité d'observer les déplacements dans le temps des limites climatiques. La teneur incontestablement élevée de carbone-13 des plantes à* C_4 *clairement indiquée dans les squelettes des animaux brouteurs, de sorte que des ossements animaux en provenance de sites archéologiques appropriés peuvent être utilisés pour observer les changements dans la composition de la couverture herbacée locale. Les observations recueillies jusqu'à présent ne laissent constater que des changements mineurs depuis le Pleistocène supérieur.*

Les données réunies à ce jour indiquent qu'en Afrique du Sud les températures et également les précipitations ont changé depuis l'apogée de la dernière période glaciaire, il y a environ 18 000 ans, mais que les déplacements des limites des divers types de veld ne furent probablement pas très importants.

INTRODUCTION

The stable isotope composition of the light elements hydrogen, oxygen and carbon provides information about the physical and chemical history of the compounds in which they occur. As a result of differences in the rates of processes in which the mixtures of isotopic molecules are involved, a small degree of isotope separation frequently takes place, and in natural systems the magnitude of the isotopic fractionation is often directly or indirectly governed by climatic conditions — specifically by temperature. By analysing the variations that occur in the ratios of the isotopes, i.e. $^2H/^1H$, $^{18}O/^{16}O$ or $^{13}C/^{12}C$, in fossil deposits evidence of past climatic change can, therefore, be derived. Measurements are usually expressed as the deviation of the isotope ratio (in per mil) from that of a standard sample,

$$\text{i.e. } \delta^{18} = \frac{(^{18}O/^{16}O)\ sa - (^{18}O/^{16}O)\ st}{(^{18}O/^{16}O)\ st} \quad (^0/_{00})$$

Negative values for δ thus denote a deficiency of the heavy isotope in the investigated material.

The most detailed information on past climatic change has been obtained from variations in the ^{18}O content of foraminifera from ocean floor cores, the analysis of which has produced a record of global

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ocean temperature changes through the Quaternary and beyond (e.g., Shackleton & Opdyke, 1973).

The effect of these global fluctuations in temperature on the continental climates depends on locality and must be determined separately for each region. The use of isotope analyses for this purpose is still in the developmental stage and has not yet produced spectacular results. One reason for this is the scarcity of suitable terrestrial materials which, it should be pointed out, must also be accurately datable by radiocarbon or other means. *Ice cores* from Greenland and Antarctica have provided excellent records of the change in the isotopic composition of precipitation (^{18}O) during the late Quaternary (Johnsen *et al.*, 1972). Such profiles can, of course, only be obtained in the polar regions. On the other continents the calcium carbonate deposits in caves (*speleothems*) offer good prospects (Hendy & Wilson, 1968). The problem here, however, is that the ^{18}O content of the carbonate is dependent both on the temperature of crystallization and on the ^{18}O content of the precipitation at the time of formation so that a temperature record cannot be derived without involving certain assumptions. Thirdly the deuterium content of *peat* has been shown to preserve a record of the changes in the isotopic composition of surface water (precipitation) with time (Schiegl, 1974), but the possibilities have not been further exploited. Finally, it has been suggested that the ^{18}O content of the phosphate (apatite) in fossil *bones* can also provide a record of climatic change in the past (Longinelli & Triglia, 1981).

CLIMATIC CHANGE ON THE SUB-CONTINENT

Isotopic evidence for climatic change on the southern African sub-continent is still very limited. At present we are concentrating our efforts on documenting the effects of the major increase of temperature that occurred since the last glacial maximum some 18 000 years ago.

Uitenhage groundwater

Between Uitenhage and the coast, just north of Port Elizabeth, there is a confined body of underground water which is slowly moving towards the ocean. By measuring the decrease in the radiocarbon content of the dissolved bicarbonate with increasing distance from the recharge area, it could be established that this artesian aquifer contains water representing the local precipitation over the past 28 000 years (Vogel, 1970). The change in isotopic composition of the water samples with age is shown in Fig. 1. To convert the change observed in the deuterium (or ^{18}O) content at the Pleistocene/Holocene boundary into temperature, the present-day variations of the isotopic composition of precipitation may be used. The latitudinal dependence of the average ^{18}O composition of precipitation at Atlantic coastal and island stations is shown in Fig. 2 (IAEA, 1969). Using this relationship, and taking the change in the isotopic composition of the oceans during the Ice Age into account, it may be deduced that the temperature change at Uitenhage since the last glacial maximum corresponds to an effective decrease of some 10° in latitude which, in turn, represents an increase in temperature of about 5,5°C. This may suggest a change in climatic conditions similar to the present-day difference between Sydney and Tasmania.

Cango cave stalagmite

The data obtained for the artesian aquifer at Uitenhage may be used in a rather less speculative manner in conjunction with isotopic measurements on speleothem material from the Cango caves near Oudtshoorn. As mentioned above, the oxygen isotopic composition of the calcite of cave-stone depends on the ^{18}O content of the groundwater dripping into the cave and the temperature at which

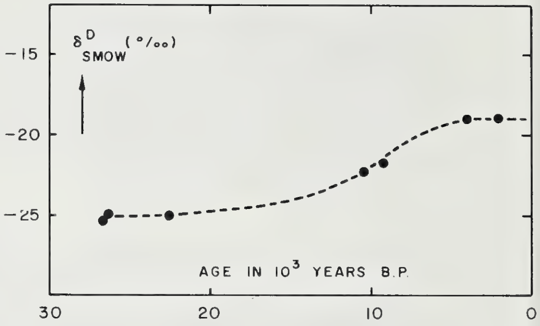

FIG. 1.—Deuterium content (δ^D) of groundwater relative to the SMOW standard, from a confined aquifer near Uitenhage, Cape Province. The age of the groundwater as determined by radiocarbon dating (Vogel, 1970), increases regularly from recent near the recharge area to 28 000 years Before Present, some 18 km down-dip. The results show a distinct change in the isotopic composition of the water between the Upper Pleistocene and the Holocene, from 6‰ in δ^D or 0,8‰ in δ^{18}

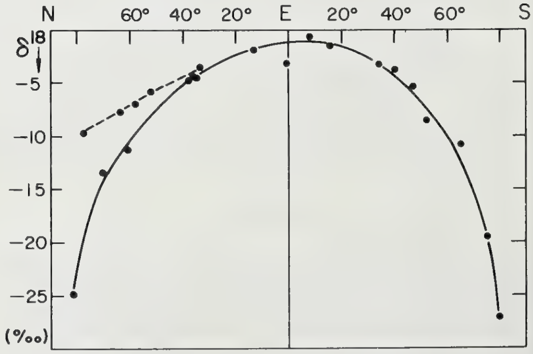

FIG. 2.—Latitudinal dependence of the average ^{18}O composition of precipitation (rel. to SMOW) at Atlantic coastal and island stations derived from data published by the Intern. Atomic Energy Agency (IAEA, 1969). The dashed line connects stations along the west coast of Europe and reflects the influence of the warm Gulf Stream on this area. Between 34°S and 44°S δ^{18} decreases by 2‰, whereas the average temperature decreases by 5 to 6°C. During the last glacial maximum δ^{18} of precipitation at Uitenhage (Fig. 1) was 0,8‰ more negative and ocean water was 1,2‰ more positive, therefore indicating a total change of 2‰ corresponding to a temperature drop of about 5,5°C.

the carbonate is precipitated from this water. If it is accepted that a shift of 6‰ in the deuterium content corresponding to 0,8‰ in ^{18}O, as observed at Uitenhage, applies generally to the southern coast of the Cape Province, temperatures of crystallization for the Late Quaternary can be calculated. For this purpose a stalagmite, 2,8 m in height, was selected from the inner part of the Cango caves. Radiocarbon analyses show that this stalagmite had developed over the past 45 000 years. The relative ^{18}O content as a function of age is given in Fig. 3. Using these data, a temperature increase since the last glacial maximum of 5°C is calculated.

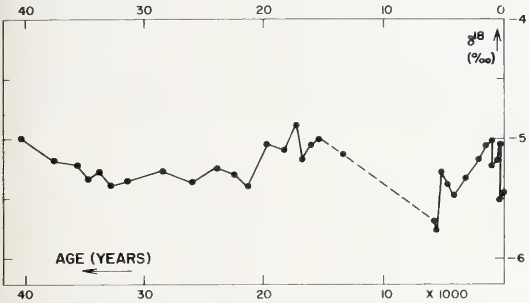

FIG. 3.—Preliminary ^{18}O analyses of $CaCO_3$ (rel. to the PDB standard) in a stalagmite from the Cango Caves near Oudtshoorn, Cape Province. Radiocarbon dating of the stalagmite shows that it has been growing in a more or less regular manner since 40 000 years ago. Samples taken along its growth axis thus provide an ^{18}O record of climatic change since Upper Pleistocene times (Vogel & Talma, in preparation.)

CHANGES IN VEGETATION PATTERNS

From a botanical point of view, the effect of climatic change on vegetation patterns is of more importance than the magnitude of the temperature change since the Last Ice Age. The widespread occurrence of grass species utilizing the C_4 pathway of photosynthesis in southern Africa provides a unique opportunity of investigating changes in their distribution with time by means of isotopic analyses.

C_4 plants are clearly distinguishable from C_3 plants on the basis of their stable carbon isotope ratio, $^{13}C/^{12}C$, and this difference in isotopic composition is in turn reflected in the bones of animals feeding on such vegetation (Vogel, 1978). Thus, for instance, the fossil bones of a grazer species such as the zebra can be used to observe the relative amount of C_3 and C_4 digested by the animal and to establish any changes in the C_3/C_4 ratio of the plant cover.

In a previous study (Vogel *et al.*, 1978) it was found that C_4 grass species were dominant in most of the summer rainfall area of the sub-continent, whereas C_3 grasses dominate the winter rainfall area of the western Cape and the summits of the mountain ranges of the eastern Cape and the Drakensberg. The distribution pattern is ascribed to differences in the temperature during the growing season — with high temperatures favouring the C_4 species, and it is to be expected that the lower temperatures prevailing during the Ice Ages would have resulted in an expansion of the C_3 grass area. To establish whether changes in this pattern in the past can be detected, fossil bone samples from two archaeological excavations situated in sensitive areas have been investigated. The first site, Melikane Cave, lies in the upper Orange River Valley in Lesotho and the second, the so-called Apollo 11 Cave, is some 50 km north of the Orange River in South West Africa/Namibia.

The average relative ^{13}C content of collagen in modern zebra bones from the C_4 grass areas in South Africa is −9,3‰ (Vogel, 1978). The results for a set of fossil zebra teeth from the archaeological excavation in Melikane Cave, Lesotho, are shown in Table 1. The two Holocene samples indicate that the diet of the animals consisted of about 35% C_3 plants, whereas the diet of the Pleistocene specimens increased to over 80% C_3. This suggests a clear shift to C_3 grass dominance in the environment of Melikane at the time, presumably due to the lower prevailing temperatures.

TABLE 1.— Carbon-13 content of collagen, δ^{13} (rel. to PDB), of collagen from *Equus* teeth of various ages, collected from archaeological excavations in Lesotho and South West Africa/Namibia. The last column lists the contribution of C_3 plants to the diet of the animals as can be deduced from the isotopic composition, δ^{13}. The results clearly show a different composition for the vegetation cover during the Upper Pleistocene

Sample	Approx. age (yrs)	δ^{13} (‰)	% C_3 in diet
	Melikane Cave, Lesotho		
MLK2	1 500	−12,8	38
MLK5	”	−12,2	34
MLK9	20 000	−18,0	75
MLK10	”	−18,3	77
MLK12	”	−18,5	79
MLK13	35 000	−19,2	84
MLK14	”	−18,2	76
MLK20	42 000	−18,8	81
	Apollo 11 Cave, SWA/Namibia		
B156/Z1	recent	−12,6	36
B157/Z2	7 000	−14,1	47
B158/Z3	20 000	−14,9	53
B159/Z4	70 000	−14,9	53

A similar set of zebra teeth from the Apollo 11 cave in southern Namibia indicates a much smaller increase in the C_3 plant component of the diet available to grazers in the area during the Upper Pleistocene (Table 1). It can therefore be concluded that the winter rainfall area along the west coast was not extended appreciably further northwards during the Last Ice Age.

Many more sites still need to be investigated, but the results gained thus far suggest that changes in the C_3/C_4 ratio of the grass cover could ultimately be reconstructed in some detail. It may also be mentioned that there are several other possible variations on this general theme; for instance, springbok bones from suitably situated archaeological sites could be used to reveal shifts in the boundary between the Karoo flora and savanna during past changes in humidity. It, therefore, seems clear that this new isotope tool has the potential for providing useful data on palaeoclimates and their effect on the vegetation.

ACKNOWLEDGEMENTS

I am indebted to Dr D. Bredenkamp of the then Department of Water Affairs for originally drawing my attention to the Uitenhage aquifer; to Mr M. Schultz, Town Clerk of Oudtshoorn for permission to remove a stalagmite from the inner part of the Cango Caves for analysis; to Prof. H. J. Deacon for his assistance during the initial stages of the project; and to Mr J. Blacquire for his invaluable help in securing the specimen. Dr W. E. Schiegl and Mr A. S. Talma performed the isotope analyses reported here, while Annemarie Fuls, Lies Lursen and Ute Kiso prepared the collagen samples for measurement.

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Long distance dispersal, overland migration and extinction in the shaping of tropical African floras

F. WHITE*

ABSTRACT

The distribution, ecology, probable modes of dispersal and taxonomic relationships of five species of Chrysobalanaceae and one of Meliaceae and Hernandiaceae are summarized. Most of these show trans-oceanic disjunctions and, in Africa, behave as ecological and chorological transgressors; morphologically they are variable. The potential importance of transgressors in the origin of new species and of evolutionary innovations, and in the interpretation of disjunctions is discussed.

RÉSUMÉ

INFLUENCE DE LA DISPERSION A LONGUE DISTANCE, DE LA MIGRATION DE PROCHE EN PROCHE ET DE L'EXTINCTION DES ESPECES, DANS LA FORMATION DES FLORES TROPICALES AFRICAINES

La répartition, l'écologie, les modes de dispersion probables et les relations taxonomiques de cinq espèces de Chrysobalanacées, d'une Méliacée et d'une Hernandiacée sont résumées. La plupart de ces espèces montrent des disjonctions transocéaniques et, en Afrique, se comportent comme des transgresseurs écologiques et chorologiques; morphologiquement, elles sont très variables. L'importance potentielle des transgresseurs dans l'origine de nouvelles espèces et de changements dus à l'évolution ainsi que dans l'interprétation des disjonctions, est discutée.

> *'Wide ranging, much diffused and common species vary most' — C. Darwin, Origin of Species (1859).*
> *'It cannot be the same species: the ecology is different' — frequently overheard in herbaria.*

INTRODUCTION

From the time of De Candolle (1855) and J. D. Hooker (for refs. see Turrill, 1953) to the present (e.g. Raven, 1972) disjunct distributions of plants have been of perennial interest to botanists, and their possible origins have been the subject of much controversy. The latter has centred largely on the relative importance of long distance dispersal and direct migration over existing and earlier land masses, followed by extinction in parts of the former range. In many cases the problem remains largely unresolved (White, in press, A). In recent years, however, rapid progress in our understanding of earth history, principally in the fields of plate tectonics and Upper Cenozoic world climatic change and deterioration, has led to renewed interest in the subject, and is providing a firmer scientific basis. There has also been an increase in our knowledge of possible modes of dispersal (e.g. Wickens, 1976) and in palaeobotany, though fossil evidence, even in the field of palaeopalynology, remains disappointingly meagre.

Important though these developments are, their value is diminished in the absence of detailed and accurate information on individual species, and on the distribution and salient features of the world's major phytochoria and vegetation types. For Africa, however, there has been significant recent progress in this area. Thanks largely to the efforts of many individual members of AETFAT, who have published monographic studies and revisions, or have contributed to regional floras or to 'Distributiones Plantarum Africanarum', and to the collective enterprise of the AETFAT Vegetation Map Committee (see White, 1976a; in press B (ed.); in press, C), the flora and vegetation of Africa are now probably better known than for most comparable parts of the tropics and subtropics. Much, however, remains to be done. Nevertheless, for several taxonomic groups, it is no longer true to say that 'taxonomic uncertainty and inadequate or uneven collecting' is a serious obstacle to biogeographical reconstruction (Street, 1981), though there may be other limiting factors.

When disjunctions are discussed attention is often focused on wide disjunctions involving taxa which have narrow geographical ranges, and, despite their relatively close relationship, are nevertheless sharply distinct. Such disjunctions are likely to have a long history behind them, and the longer that history is, the more difficult it is to interpret them.

By contrast, the present study is concerned with a small phytogeographical element, composed of species common to the American and African tropics, which appear to be adapted to dispersal by ocean currents, but also have extensive distributions in the interior of the continents, where they occur in several different vegetation types in two or more phytochoria. Hence they can be referred to as ecological and chorological transgressors (White, 1979). They are also very variable in their morphology and are either polytypic or are ochlospecies (White, 1978a). In studying such species, we are seeing evolution in action. Without adopting the doctrine of uniformitarianism in its extreme form, it is clear that situations such as these

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have much to tell us, not only about the nature of disjunctions, but also about the ways in which new taxa and evolutionary innovations arise. A knowledge of such species should also help to guide us in the interpretation of patterns which originated in the more distant past, and for which less evidence remains.

Three species, *Chrysobalanus icaco* (Chrysobalanaceae), *Carapa guianensis* (Meliaceae) and *Gyrocarpus americanus* (Hernandiaceae) are chosen to illustrate this theme. Their families have recently been monographed or are undergoing monographic revision. In order to cover the subject more comprehensively, four additional genera of Chrysobalanaceae, *Hirtella, Licania, Neocarya* and *Parinari,* are briefly mentioned. Within the single species *Chrysobalanus icaco,* perhaps we can see the beginnings and early stages of the evolution of an obligate strand plant. In the Meliaceae tribe Xylocarpeae, we can see both the beginnings and the end product, and for that reason, the mangrove genus *Xylocarpus* is considered alongside its close relative *Carapa.*

CHRYSOBALANACEAE

Of the 454 species in this pantropical woody family, 349 occur in America, 61 in Africa, of which two, *Chrysobalanus icaco* and *Parinari excelsa*, are shared with America (see below), and 46 in Asia and the Pacific. It is probably this striking disparity in floristic richness between the Old and the New Worlds that has led some authors (Raven & Axelrod, 1974, p. 585) to postulate an American origin for the group. This is contradicted, however, by the fact that of the 17 genera all but 3 occur in the Old World and 9 are confined to it.

The fruit of Chrysobalanaceae is remarkably uniform in basic construction, though dispersal mechanisms are diverse, including transportation by fresh and sea water. The Chrysobalanaceae is one of the few pantropical families that have been comprehensively revised in recent times (Prance, 1972; White; 1976; Prance & White, in prep.).

Chrysobalanus

Two species are currently accepted (Prance & White, in prep.) — the amphi-atlantic *C. icaco,* and *C. cuspidatus,* which is confined to the Windward & Leeward Islands (Fig. 1). Two subspecies are recognized in *C. icaco,* which is a transgressor, occurring in a wide range of vegetation types.

C. icaco subsp. *icaco* is widespread in the coastal regions of tropical and subtropical America from Florida to southern Brazil, and along the Atlantic seaboard of Africa from Senegal to Angola. Both in America and Africa it occurs mainly in coastal thicket on sandy shores, often immediately above the strand line. But it is also found on the landward side of mangrove swamps and further inland (up to 200 km in Africa and 600 km in South America) on the banks of rivers and in waterlogged wooded grassland (savanna).

C. icaco subsp. *atacorensis* is confined to Africa, where it is widely distributed in the interior of the continent on the banks of rivers, mostly in the Guineo-Congolian rain forest region, but also in scattered localities in fringing forest far to the north and south of the main blocks of rain forest.

The leaves of subspp. *icaco* and *atacorensis* are very different. Those of the former are coriaceous and orbicular; those of the latter are thinner and acuminate. Intermediates are found, however, wherever the two subspecies come into contact all the way from Liberia to Angola.

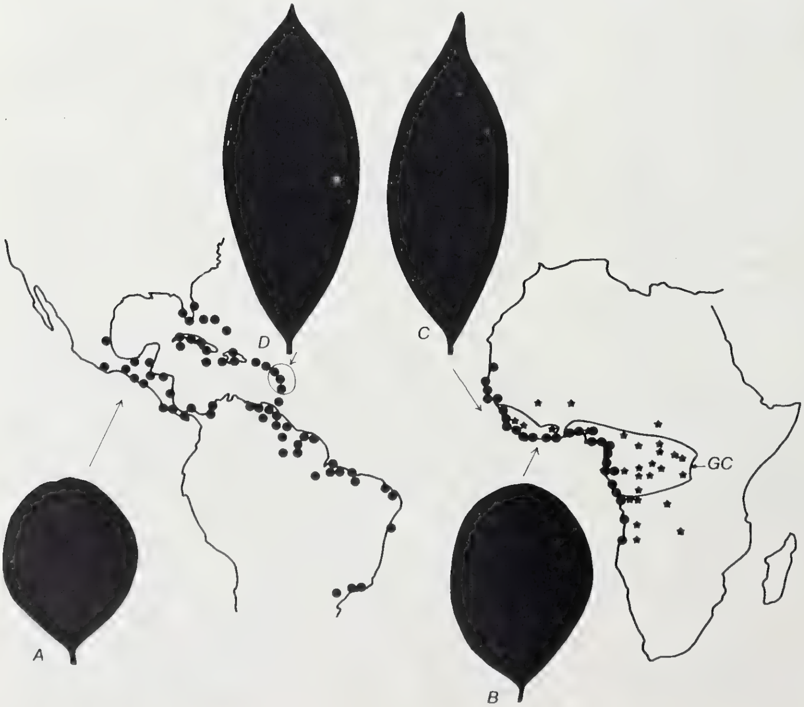

FIG. 1.—Pictorialized distribution map of *Chrysobalanus icaco* subsp. *icaco* (circles) and subsp. *atacorensis* (stars), and *C. cuspidatus* (distribution indicated by line encircling Windward and Leeward Islands) — after Prance (1972) and White (1976b, 1976c). A, *C. icaco* subsp. *icaco (Standley* 22023, El Salvador); B, *C. icaco* subsp. *icaco* (*Jacques-Félix* 7314, Guinea); C, *C. icaco* subsp. *atacorensis* (*Dawe* 44, Angola); D, *C. cuspidatus* (after Fl. Neotr. 9, Chrysobal., fig. 2) GC indicates the limits of the Guineo-Congolian Region. All leaves × 0,5.

In leaf-shape, *C. cuspidatus* and *C. icaco* subsp. *atacorensis* are similar, though there are differences in the inflorescence. The former is also a forest species, though in this case, it inhabits stunted forest on the crests of wind-swept ridges, where it forms up to 30 per cent of the stand. No intermediates have been found between *C. cuspidatus* and *C. icaco* subsp. *icaco*.

The pattern of relationships described above is complex as must also be its origin. Several alternative explanations can be offered to explain its origin, but the evidence available is indecisive. Leaving aside the less probable hypotheses it can be concluded that, *either* both the forest and the coastal forms have independently crossed the Atlantic at some time in the past, *or* that the forest form represents the primitive condition on one side of the Atlantic and has originated independently on the other side by reversion, and de-specialization.

The fruit of *C. icaco* is a fleshy drupe, which is dispersed by bats and ocean currents. It is buoyant because the seed, which can remain viable after the fruit has floated for two months, does not entirely fill the cavity of the endocarp. Large numbers of the latter can be found among the shore-line flotsam.

Hirtella

There are 92 species, of which 91 occur in tropical and subtropical America (Fig. 2). The remaining species, *H. zanzibarica,* occurs in East Africa and Madagascar. On the African mainland it is represented by subsp. *zanzibarica,* whilst four geographically replacing subspecies occur in Madagascar. Subsp. *zanzibarica* is a transgressor. It is widespread in fringing forest and various types of lowland forest, but in Tanzania it also ascends to 1950 m where it occurs in Afromontane rain forest. The closest relative of *H. zanzibarica* seems to be *H. bahiensis,* which is confined to a small area in NE Brazil.

At present it is difficult to account for the disjunct distribution of *Hirtella,* though there are parallels in other genera. This type of distribution has been reviewed by Stearn (1971), who suggested that the disjunct areas had their origin in the far distant past before the breakup of Gondwanaland. Such hypotheses can now be shown, however, to be discordant with recent views on plate tectonics and the early differentiation of the Angiosperms. Hence, it is necessary to seek alternative explanations involving both long distance dispersal and overland migration, accompanied, by extinction over a considerable area.

It is quite likely that taxa which have similar distributions today, were transported by different agents and have had quite different histories. Little is known of the dispersal of *Hirtella,* but the American species that have been studied are dispersed by birds, (G.T. Prance, pers. comn.). This would not, however, rule out the possibility of occasional trans-oceanic dispersal by currents, since the fruit of *Hirtella* is basically similar in construction to that of water-dispersed species of *Chrysobalanus* and *Licania.*

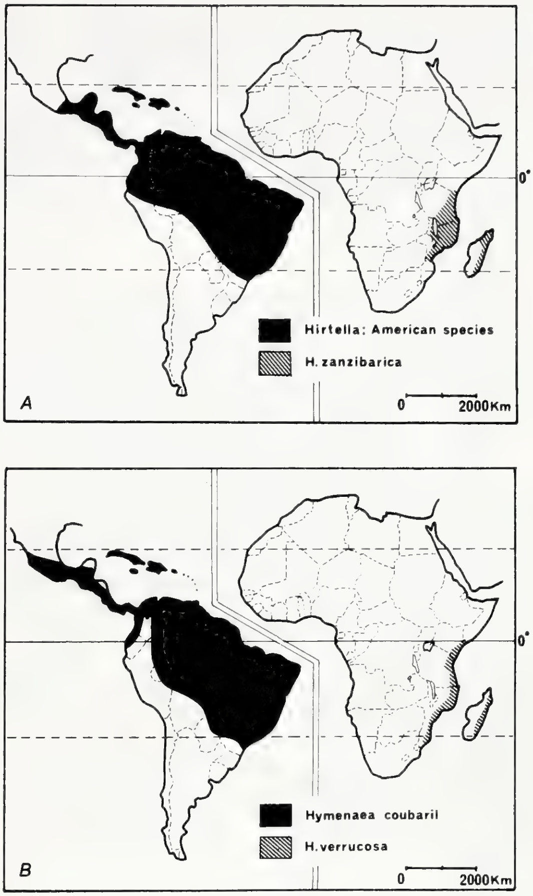

FIG. 2.—A, distribution map of *Hirtella* (after White, 1976b, 1976c, and Prance & White in prep.); B, distribution map of *Hymenaea* (after Langenheim, 1973). Note: the range of *H. coubaril* embraces those of the 16 remaining American species.

The distribution (Fig. 2B) of the genus *Hymenaea* (Leguminosae: Caesalpinioideae) is broadly similar to that of *Hirtella* (Langenheim, 1973; Langenheim & Lee, 1974; Lee & Langenheim, 1975). The only African species of *Hymenaea, H. verrucosa,* occurs in East Africa and Madagascar. It is a transgressor and its indehiscent pods are believed to be, at least in part, water-dispersed. Of the 13 American species of *Hymenaea, H. couburil* is widely distributed in Central and South America and the West Indies. It also is a transgressor, and morphologically is very variable. Its pods are frequently encountered in drift and its seeds are said to retain their viability for several years. According to Lee & Langenheim (1975) ocean-dispersed pods of *Hymenaea* (species not stated) are commonly found along the southern shores of Florida. Seeds from this source were found to germinate within 7 – 10 days.

Despite the great disparity in number between the neotropical and African species, Langenheim and Lee believe that *Hymenaea* originated in Africa. They discuss the evidence for this at some length, but the pattern of relationships shown by the African and American taxa, as in *Chrysobalanus* (p. 396

and *Gyrocarpus* (p. 401), is complex, and evidence concerning the history of the group appears to be equivocal. The Leguminosae (including *Detarieae),* however, are good dispersers (Raven & Polhill, 1981), and the possibility that *Hymenaea* might have entered Africa from America cannot be ruled out on present evidence. *Hymenaea* is closely related to the neotropical genus *Peltogyne* which has typical, dehiscent leguminous pods.

Licania

There are c. 170 species. *L. elaeosperma* is confined to Africa, and two species occur in the forests of the Far East. All the others are neotropical in distribution (Fig. 3). The African and Asiatic species are sufficiently different from the American to require separate subgenera, *Afrolicania* and *Angelesia* respectively, to accommodate them.

Most of the American species occur in lowland rain forest, where 30 of them are characteristic of seasonally inundated forest, especially *várzea* forest of the Amazon basin. The fruits of some swamp forest Licanias are eaten by fishes (Gottsberger, 1978; Goulding, 1980). The stomachs of a large fish, *Lithodoras dorsalis,* have been found to be stuffed full of the fruits of *Licania longipetala,* which are capable of floating for two or three days. When the fruit skin is perforated or is penetrated by water the fleshy mesocarp, which acts like an air sack, disintegrates and the seeds sink. It is believed that the fish feeds at night and is an important dispersal agent. 'Seeds' (? endocarps) stripped of their fleshy covering, pass through the fish unharmed; those removed from the lower intestines germinated in experimental pots.

L. elaeosperma occupies a narrow coastal strip in West Africa from Guinea to Gabon. It occurs principally at the landward side of mangrove swamps and, further inland, in periodically flooded riparian forest. Its fruits are dispersed by water, but it is not known whether they are eaten by fishes.

L. elaeosperma has no close relatives in America, but it is possible that it is descended from a now extinct American swamp forest species, the fruits of which were transported across the Atlantic. The taxonomically isolated position of *L. elaeosperma* might be due to the extinction in Africa of other species which formerly provided connecting links between it and the species now occurring on other continents.

It has long been suspected that fishes can effect dispersal, but the extent and importance of this phenomenon have only recently been established (Goulding, 1980). Much remains to be discovered, however. Most fruits eaten by fishes in Amazonia are buoyant and 'buoyancy may be the most important overall mechanism of the flooded forest community for seed dispersal' (Goulding, p. 225). 'The ecological significance of buoyancy', however, 'in relation to predation and dispersal by fishes is not without its mysteries' (*tom. cit.,* p. 226). *Licania* is one of many amphi-atlantic genera with swamp forest species on one or both sides of the Atlantic. Even though the origin of buoyancy and the significance of fishes are imperfectly understood, there can be little doubt that buoyancy of fruits as an adaptation to swamp forest conditions has pre-adapted many genera to transoceanic dispersal.

Neocarya

N. macrophylla, the only member of its genus, is mentioned because, although it is confined to Africa, it is a transgressor with an unusual distribution (Fig. 4). It is common in West Africa in a coastal strip up to 300 km wide extending from Senegal to Liberia. It also has a scattered east-west distribution in the much drier and more continental northern half of the Sudanian Region 700–1 000 km inland. Throughout its range it seems to be confined to sandy soils. Its Sudanian distribution is presumably relictual from a wetter epoch. Other species, which resemble *N. macrophylla* in being abundant in the wetter subcoastal parts of West Africa and also have relictual populations inland, are discussed by Jaeger (1959). Among the latter, the best-known is *Guibourtia copallifera,* which is locally dominant on the sandstone escarpment of Bamako (Mali), where *N. macrophylla* also occurs. Notwithstanding its diverse ecology, in morphology, *N. macrophylla* is not very variable.

Parinari

Forty-four species are currently accepted, 18 in tropical America, 6 in tropical Africa and the remainder in tropical Asia eastwards to Polynesia (Fig. 5).

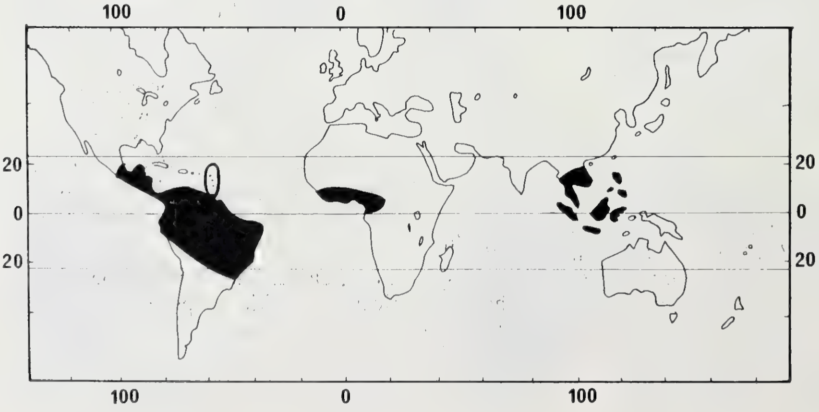

FIG. 3.—Distribution map of *Licania.*

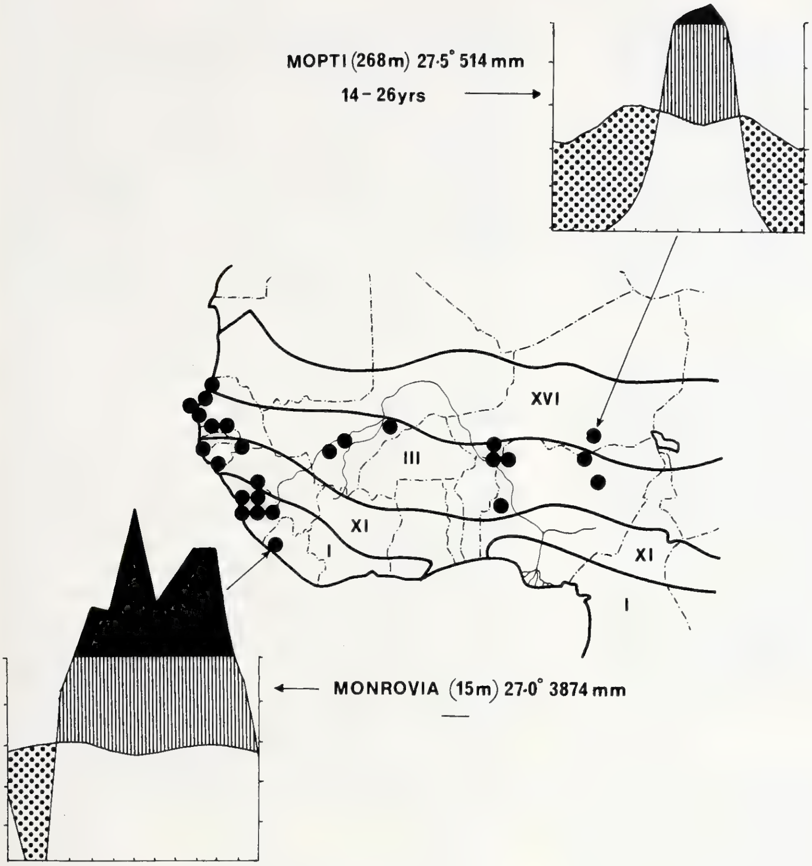

FIG. 4.—Distribution map of *Neocarya macrophylla* (after White, 1976b, 1976c) with climatic diagrams for two stations. I, Guineo-Congolian Region; XI, Guinea-Congo/Sudania transition zone; III, Sudanian Region; XVI, Sahel transition zone.

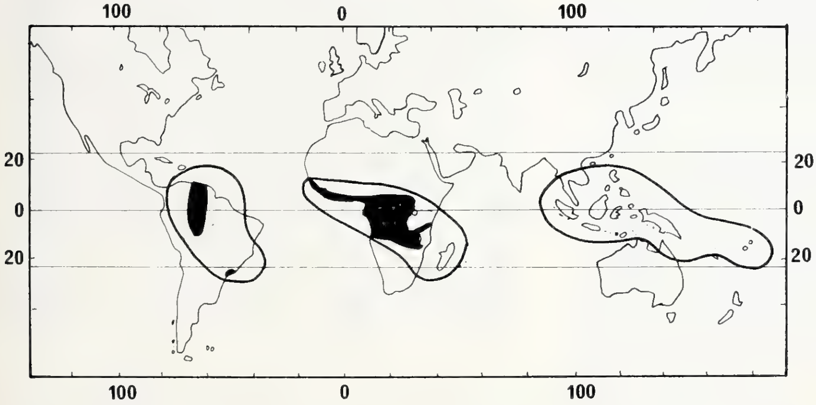

FIG. 5.—Distribution map of *Parinari*. *P. excelsa* (after Prance, 1972 and White, 1976b, 1976c) is shown in black.

Most species occur in lowland rain forest, though some are found in other forest types, in woodland and in wooded grassland. The most widely distributed American species, which extends from Colombia to south-east Brazil, is thought to be conspecific with the African *P. excelsa*. The African species are closely related to one another, but each one is at least partly sympatric with from one to four others. The evergreen forest species *P. excelsa*, the woodland species *P. curatellifolia* and the geoxylic rhizomatous suffrutex *P. capensis* are extremely similar in the structure of their leaves, flowers and fruits, despite their widely divergent habits and ecology. Their geographical ranges show substantial overlap and intermediates of putative hybrid origin are virtually non-existent. In Africa, *P. excelsa* is a transgressor. It is widespread in Guineo-Congolian lowland rainforest, in Afromontane rain forest and in Zambezian dry evergreen forest, as well as occurring, often abundantly, in other vegetation types. Morphologically, however, it is rather uniform in Africa, but is much more variable in America. In Africa *P. excelsa* is said to be dispersed by bats, elephants and monkeys. There is no evidence that the fruits of *Parinari* can be successfully transported by ocean currents, but, in view of the importance of that means of dispersal elsewhere in the family (Prance & White, in prep,), it is likely that such a mechanism has been effective in the past.

MELIACEAE

In this family there are 51 genera and c. 550 species (Pennington & Styles, 1975). Most genera have relatively restricted distributions. *Trichilia*, alone, is pantropical. Only two genera, *Guarea* and *Carapa,* occur in Africa and the neotropics, whereas four, including *Xylocarpus,* occur in Africa and the Far East.

In my opinion, *Carapa* consists of a single ecologically and morphologically variable species. It is an ochlospecies and an ecological and chorological transgressor. Its seeds are adapted to dispersal by fresh water, and in all probability are also successfully transported by ocean currents. It is, however, essentially an inland plant, although in a few places, it occurs sporadically on the littoral itself. *Xylocarpus* is closely related to *Carapa,* but its 2 or 3 species are obligate members of coastal communities and are extremely highly specialized for dispersal by sea water. *Carapa* and *Xylocarpus* are allopatric. An interval of 700 km separates their ranges.

Carapa and Xylocarpus

These genera are closely related and collectively form the tribe *Xylocarpeae.* They have often been united in the past, but no difficulty is experienced in separating them. Ecologically they are very different. *Carapa* is widely distributed in rain forest in tropical America and in West and Central Africa, whereas *Xylocarpus* occurs in mangrove and other coastal habitats from East Africa to Polynesia (Fig. 6).

In *Carapa*, species delimitation is weak and there has been persistent uncertainty concerning their number. Two species, *C. guianensis* and *C. procera,* are currently accepted for America (Fl. Neotr., Meliaceae, p. 406), of which *C. procera* is also widely distributed in Africa. A second African species, *C. grandiflora* is also sometimes recognized. In my opinion, it is doubtful whether these taxa can be upheld, at least at specific rank. It seems better for present purposes, to recognize a single variable species.

In the neotropics *C. guianensis* is distributed throughout most of the Amazon basin and northwards to Central America. It is also widespread in the Greater and Lesser Antilles but is absent from Jamaica and most of Cuba. On the mainland it is mostly confined to rain forest regions in which its favoured habitat is swamp forest, but it also occurs on well-drained soils. In Venezuela it ascends on mountain slopes to 1 400 m. *C. guianensis* is usually found in the understorey, rarely in the canopy, of rain forest and swamp forest, but in Dominica it has been reported from scrubby windswept forest.

In Africa this species is widely distributed in lowland rain forest of Guineo-Congolian type from Senegal to the Lake Victoria Basin. It also extends in riparian forest a short distance to the north and south of the main forest blocks, and is found on the island of S. Tomé in the Gulf of Guinea, some 300 km from the African mainland. As in America, so in Africa, the most characteristic habitat of *C. guianensis* is lowland swamp forest, but it occurs, though less plentifully, where drainage is better. It is also often abundant on some of the African mountains, namely those of the Kivu-Ruwenzori system (White, 1978b) and in the Cameroun-SE Nigeria Highlands. It ascends to 2 200 m and is a conspicuous component of Afromontane communities.

Carapa guianensis is extremely variable in its morphology. In habit it is usually erect, though frequently mis-shapen. In America it often attains and sometimes exceeds a height of 30 m, though in Africa 20 m is usually its upper limit. Tall trees are richly branched, but in the forest understorey it often flowers and fruits precociously in the juvenile unbranched pachycaul stage when only a few metres high. Sometimes it shows an extraordinary habit with widely divergent arcuate branches which bend down to the ground, where they then take root and grow up again.

Other variable features concern leaf-length,

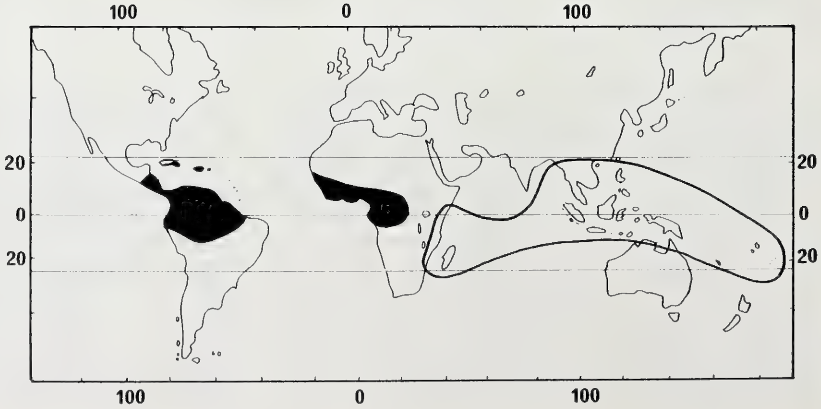

FIG. 6.—Distribution map of *Carapa* (black) and *Xylocarpus* (encircled).

number, size and shape of leaflets, inflorescence-branching, flower-size, and number of floral parts and seeds. Variation in these characters is poorly correlated, both among the characters themselves and with geography and ecology, though some variants are confined to, or occur plentifully in, certain geographical areas of restricted extent and might possibly serve in the recognition of weakly defined infraspecific taxa. The overall pattern, however, is clearly polytopic and indicates that most, possibly all, character states have arisen independently in several different places.

The seeds of *C. guianensis* are eaten by rodents, monkeys and wild pigs, which presumably are mostly destructive. They, or other animals, must, at least occasionally effect dispersal, otherwise the occurrence of *C. guianensis* on high mountains would be difficult to explain. In fresh water swamps and on the banks of rivers the buoyant seeds are transported by water, and have been observed to germinate on the white sand beaches of the Rio Negro (T. D. Pennington, pers. comm.). In Amazonia they are also eaten by fishes (Gottsberger, 1978), but it is not known whether they are ever dispersed by this means. That *Carapa* can be transported by ocean currents is shown by the occurrence of seeds in drift at Pointe Noire on the west coast of Africa (Muir, 1937), and on the shores of Yucatan (B. T. Styles, pers. comm.). It is not known whether such seeds are viable, but it seems likely that oceanic transportation has been responsible for the occurrence of *Carapa* on both sides of the Atlantic.

Although *C. guianensis* probably owes much of its present-day geographical distribution to dispersal by sea water, it seems to occur only exceptionally in coastal habitats. There are a few records, both for America and Africa, from the inner margins of mangrove, but fresh-water swamp forest further away from the coast seems to be a more characteristic habitat. There is, however, one record from the edge of the sea itself. Thus Letouzey (No. 14950) found it growing in Cameroun with *Terminalia catappa* on black volcanic sand just above high-water mark. *T. catappa,* although not indigenous to Africa, is widely naturalized along the West African coast, and is a sea-dispersed species *par excellence.*

The buoyancy of the seed of *Carapa* is due to its light, woody arilloid, which is probably homologous with the fleshy arilloid of *Trichilia* and its relatives, and with the seed wing of *Entandrophragma* and other Swietenioideae. In *Xylocarpus* specialization for water-transport is carried much further. The arilloid is thicker, angular in shape and corky in texture. There is no dormancy and the seeds begin to germinate as soon as they are released into water. According to Troup (1921) it is the germinating seedling, not the dormant seed, that is the unit of dispersal. The thickness of the arilloid is very uneven, but is thinnest at the micropyle. The seed is so constructed that it always floats in a position such that, when the seedlings breaks through, the radicle is submerged and the plumule is emergent from the water (F. White, pers. obs.). Two species of *Xylocarpus* occur in mangrove swamps and have pneumatophores or ribbon-like breathing roots; the third is a plant of sandy and rocky coasts.

HERNANDIACEAE

This family, which has been recently monographed (Kubitzki, 1969), consists of four genera and 58 species. Some species of *Gyrocarpus* and *Hernandia* are widely distributed by ocean currents.

Gyrocarpus

Several species have been described, but Ridley (1930) thought they were all forms of one, the pantropical *G. americanus*, except possibly for *G. hababensis,* which is confined to the Horn of Africa (Fig. 7). Kubitzki keeps a third species, *G. jatrophifolius* separate. It occurs in Mexico and Central America from sea level to 1 800 m, and its range overlaps slightly with that of *G. americanus.* Within the pantropical *G. americanus* Kubitzki recognizes eight, mostly allopatric, but partly overlapping subspecies.

As in *Chrysobalanus icaco* and in *Carapa guianensis*, so in *Gyrocarpus americanus,* we are dealing with a taxon which shows at least one transoceanic disjunction and occurs in diverse habitats in the continental interior. In *Gyrocarpus,* however, the distribution is fragmented, especially in Africa, and the overall pattern of taxonomic relationships is somewhat complex. There can be

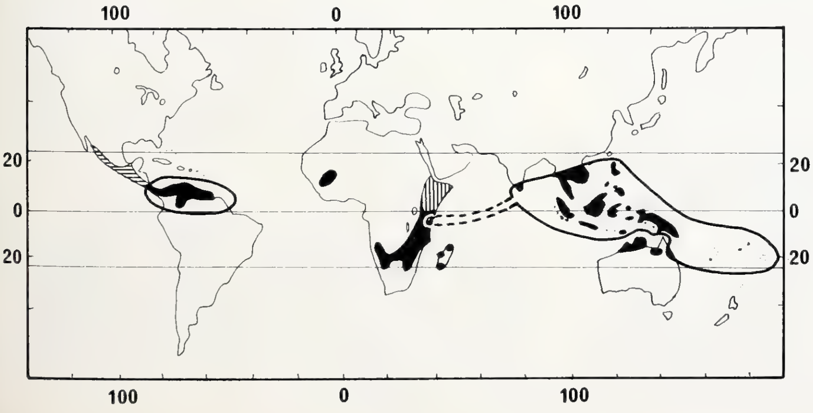

FIG. 7.—Distribution map of *Gyrocarpus. G. jatrophifolius* (horizontal lines); *G. hababensis* (vertical lines); *G. americanus* (black, with subsp. *americanus* encircled). After Kubitzki (1969).

little doubt that this complexity is the result of a complex history involving several different successful dispersals between widely separated regions, followed by expansion of range and much subsequent extinction. In a detailed and interesting analysis Kubitzki has attempted to unravel this history, based largely on the geographical distribution of certain 'unidirectional trends'. The differences between taxa in *Gyrocarpus*, however, are so slight that the possibility of a reversal of trends must be borne in mind.

One of the Kubitzki's conclusions is that sea-dispersal in *Gyrocarpus* has been relatively recently acquired, and that some intercontinental disjunctions are of Gondwanic origin. For reasons given elsewhere (White, in press A) it now seems unlikely that many extant genera of Angiosperms were in existence before Africa separated from South America in the Cretaceous. It seems much more likely that there were early transoceanic dispersals of *Gyrocarpus* that were perhaps 'accidental', and that subsequently, in certain parts of its range, but not in all, *Gyrocarpus* became adapted, at least facultatively, to coastal habitats, and hence more dependent on transportation by sea water.

Kubitzki, following a remark of Chevalier (1938) and others, suggests that the present distribution in West Africa of *G. americanus* subsp. *pinnatilobus* might be located near an ancient shore-line, but there seems to be little geological evidence for this. The fact that *G. americanus* subsp. *africanus* south of the equator, has a scattered distribution right across Africa, shows that this species is capable of crossing continents. The isolated position of subsp. *pinnatilobus,* north of the equator, is presumably relictual from a former, wider distribution.

In inland localities the winged fruits of *Gyrocarpus* are dispersed by wind or (down stream) by streams and rivers. Fruits which find their way to the sea can drift to distant coasts and to islands, since they can float and remain viable for at least two months (Ridley, 1930).

Gyrocarpus americanus occurs as a strand plant in only part of its range. In the Far East it is widespread from India, Ceylon and the Cocos Islands to Fiji, Samoa and Tonga, and is often abundant near the shore. Nevertheless, it has an unpredictably patchy distribution in this part of the world and is by no means confined to coastal habitats. On Christmas Island, New Guinea and Tahiti it ascends to 700 m.

In America, *G. americanus* occurs both in coastal habitats, e.g. in coastal thicket with *Spondias mombin* in Venezuela (Aubréville, 1949), and inland, where it is a characteristic member of dry deciduous woodland (A. M. Sugden, pers. comm.). It is absent from the Greater and Lesser Antilles.

In Africa all known stations are from the interior. Even in the East African coastal belt, *G. americanus* subsp. *americanus*, the typical strand variant, occurs, not on the shore, but in various types of forest, some distance from the shore itself.

Ecologically, *G. americanus* is very versatile. It occurs in a wide range of forests, woodlands, bushlands and thickets.

DISCUSSION

Of the seven species described above, one, *Licania elaeosperma*, is taxonomically isolated, ecologically specialized, and has a restricted distribution; it is clearly a relic. All the others are ecological and chrological transgressors, and all but one, *Neocarya macrophylla,* are extremely variable. *Chrysobalanus icaco, Hirtella zanzibarica* and *Gyrocorpus americanus* are polytypic, whereas *Parinari excelsa* and *Carapa guianensis* are ochlospecies.

The study of morphologically variable transgressors can contribute much to our understanding of the past, but it should be remembered that at any one time their number is likely to be small. Thus, White (1979) has estimated that only 1,6% of Guineo-Congolian species come into this category, whereas Hall & Swaine (1981), adopting a more elastic concept, regard 12% of the Guineo-Congolian flora in Ghana as transgressors. Also, in the past, transgressors might have shown very different patterns of relationship.

For at least 40 years zoologists have had clear ideas on the predominant mode of speciation — geographical or allopatric speciation — in the animal kingdom, though its universality has recently been questioned (see M. J. D. White, 1978). Nevertheless, 'it is now widely accepted that in most animal groups this is the main, or indeed the only, way in which speciation takes place' (Snow, 1981).

Although botanists have paid lip-service to geographical speciation, for the most part, they have concentrated on such topics as ecotypic differentiation, clinal variation and introgression, which it now seems are relevant to only a small part of the story. My own experience of the African flora leads me to believe (e.g. White, 1955, 1962) that geographic speciation, at least for the larger woody plants, is the predominant mode. I would like to suggest that transgressors, such as those discussed in the present account, when studied with their closest relatives in a monographic context, provide important evidence on ways in which geographical speciation can be brought about. The interest of transgressors, however, is much wider than this, for they can also reveal clues concerning the origin of important evolutionary innovations, and changing patterns of plant distribution, both in the relatively recent and more distant past.

Finally, it should be emphasized that the transgressors described above represent only a small selection of those that exist. I have concentrated on those which show wide trans-oceanic disjunctions. There are many others which are confined to the African mainland or to Africa and its offshore islands, including Madagascar (see for instance White, 1978a; in press, A).

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Vegetation geographical patterns as a key to the past, with emphasis on the dry vegetation types of South Africa

M. J. A. WERGER*

ABSTRACT

Southern Africa is characterized by a highly diversified vegetational cover with extremes as contrasting as desert, tropical forest, alpine grassland, or mediterranean type scrub, and many other types in between. This vegetational pattern is strongly correlated to the climatological pattern. It is therefore likely that past changes in climate can still be partly traced in the vegetational pattern, particularly in geographical anomalies, and that study of these patterns provides complementary evidence to palynological research. The following anomalies in the vegetational pattern are briefly discussed:

1. island-wise occurrence of Afro-montane vegetation on mesic, sheltered sites in the southern Sudano-Zambezian Region, in particular in the Highveld grassland/False Karoo transition area;
2. similar westward occurrence of Sudano-Zambezian scrub patches in the Karoo-Namib Region near the Orange/Vaal confluence;
3. scattered occurrence of Sudano-Zambezian woody species in a matrix of Karoo-Namib vegetation in the marginal Karoo-Namib Region;
4. island-wise occurrence of frost-tolerant, dry, karroid dwarf shrub vegetation of predominantly C_3-plants on isolated peaks in the winter rainfall area of Namaqualand;
5. peculiar patchy distribution of some succulents in wide areas of climatically rather homogeneous, succulent dwarf shrub vegetation of predominantly CAM-plants in the escarpment area of Namaqualand, a pattern reminiscent of that in many Cape fynbos species.

Interpretation of these patterns logically leads to the conclusion that these result from a previously wetter, a previously cooler, or a previously wetter and cooler climate, respectively, over the parts of southern Africa under discussion. This conclusion is compared with published palynological views.

RÉSUMÉ

LE PASSÉ MIS EN LUMIÈRE PAR L'ANALYSE GÉOGRAPHIQUES DES ASPECTS DE LA VÉGÉTATION, EN S'APPUYANT SUR LES TYPES DE LA VÉGÉTATION SÈCHE DE L'AFRIQUE DU SUD

L'Afrique de Sud est caractérisée par une couverture végétale très diversifiée avec des extrêmes aussi contrastés que le désert, la forêt tropicale, les formations herbeuses alpines ou les formations brouseilleuses de type méditerranéen et beucoup d'autres formations intermédiaires. Ce profil de la végétation est en étroite corrélation avec celui du climat. Il est par conséquent vraisemblable que les changements de climats du passé puissent encore être partiellement observés dans les aspects de la végétation, particulièrement dans les anomalies géographiques et que l'étude de ces aspects puisse fournir des arguments complémentaires à ceux de la recherche palynologique. Les anomalies suivantes des aspects de la végétation sont brièvement discutées:

1. *Existence d'îlots de végétation afromontagnarde dans des sites abrités et à humidité moyenne dans le sud de la Région soudano-zambézienne, en particulier dans la zone de transition de la formation herbeuse du Highveld et du Faux Karoo;*
2. *Existence vers l'ouest, de formation brouseilleuse soudano-zambézienne dans le Région du Karoo-Namib près du confluent du Vaal avec l'Orange;*
3. *Existence à l'etat dispersé d'espèces ligneuses soudano-zambéziennes dans une trame de végétation Karoo-Namib, dans la Région du Karoo-Namib marginale;*
4. *Existence sous forme d'îlots d'une végétation arbustive naine, sèche, karroïde, résistant à la gelée et componée de plantes à prédominance C_3 sur les pics isolés dans la région à pluies hivernales du Namaqualand;*
5. *Une répartition particulière sous forme d'îlots de certaines succulentes dans de vastes régions à végétation arbustive naine crassulescente à climat plutôt homogène, composée de plantes à prédominance CAM dans la zone d'escarpements du Namaqualand, aspect rappelant celui de nombreuses espèces de fynbos du Cap.*

L'interprétation de ces aspects conduit logiquement à la conclusion qu'ils résultent respectivement d'un climat antérieurement plus humide, antérieurement plus froid ou antérieurement plus humide et plus froid, qui a régné sur ces parties concernées de l'Afrique du Sud. Cette conclusion est comparée avec les considérations palynologiques qui ont été publicés.

INTRODUCTION

In all of Subsaharan Africa, South Africa stands out due to its great diversity of vegetation types. Within relatively short distances, one finds such extremes as, for example, desert vegetation, tropical lowland and montane forest, savanna woodland, mediterranean type scrub and alpine grasslands, and several transitions between these types. The distributional pattern of these various vegetation types is strongly correlated with the climatological pattern.

On the south-western edge of the country, between the coast and the escarpment, which is up to about 2 000 m high, there is a winter rainfall regime, eastwards passing into a uniform, all-year

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rainfall regime. This area is covered by the mediterranean type scrub and heathlands; only here and there we find forest-vegetation of Afromontane affinity in this area. Going northwards, the west coast and the western escarpment remain under the winter rainfall regime until well into South West Africa (Namibia), but total rainfall drops to just a few centimetres per year on average and its reliability strongly decreases, thus causing desert and semi-desert conditions.

South Africa's interior, the east coast and the northern part of the country, all fall entirely within the summer rainfall regime. Isohyets in this part of the country generally run north-south and there is an increase in average annual precipitation from about 200 mm at about 700 km away from the west coast to considerably over 1 000 mm near the east coast. In parts of the eastern escarpment formed by the Drakensberg, the rainfall can reach 2 000 mm per year (Schulze & McGee, 1978; Killick, 1978).

The vegetation accordingly shifts mainly in an eastern direction away from the west coast, from desert and semi-desert dwarf shrub vegetation to zonal grassland, montane grassland and scrub with locally montane forests to alpine vegetation on top of the escarpment, and again scrub and woodland vegetation lower down the escarpment towards the east coast, where occasionally some coastal forest is still found. Towards the northern parts of South Africa the effects of proper tropical conditions increase, and the vegetation becomes mainly a savanna woodland, forming the southern edge of the vast Sudano-Zambezian phytogeographical region (Werger & Coetzee, 1978).

The broad correlation between climate and vegetation is clear from this general picture, but more detailed climatic factors can also be correlated with distribution of the vegetation. In the dry western part of South Africa, for example, the vegetation of the coastal belt and the escarpment zone is strongly succulent, except for the highest mountain reaches, where frosts of more than 4 or 5 degrees occur regularly. On these higher parts of the mountains the vegetation becomes dominated by sclerophyllous, small-leaved karroid dwarf shrubs. Beyond the escarpment zone on the interior plateau, in the area where the uniform, all-year rainfall regime passes into the summer rainfall regime, we again come into an area with regular frosts of similar severity and again see the vegetation change from a succulent dwarf shrub vegetation to a sclerophyllous, small-leaved dwarf shrub vegetation (compare Werger, 1978a). Much further eastwards, about half-way between the west and the east coast, in the Upper Orange River area, there is a climatic boundary approximately indicated by the 400 mm isohyet, which coincides remarkably well with the borderline between the true Karoo-Namib dwarf shrub communities, the Pentzietea incanae, and the more grassy, and in their affinity more Sudano-Zambezian, karroid communities, the Pentzio-Chrysocomion and the Rhoetea erosae communities (cf. Werger, 1980).

Many more, and probably even more striking examples could be mentioned. Most of these examples will illustrate that, although there is a correlation between the distribution of the vegetation and of the various soil types, generally speaking the correlation between climate and vegetation is much more pronounced (see also Coetzee & Werger, 1975).

The strong correlation between the distributional patterns of climate and vegetation suggests that past changes in climate, especially the most recent and significant ones, may have left their marks on the distributional pattern of the vegetation, and that it is likely that such climatic changes, in part can still be traced in the present vegetational pattern. These marks will be clearest in geographical anomalies in the distribution of plant species and vegetation types, which is not to say that each such anomaly must be interpreted in terms of past climatic changes.

I shall discuss a number of surprising, aberrant distributional patterns in vegetation types which, at first sight, are difficult to explain. They may be interpreted as possible traces of relatively recent climatic changes and the logical conclusions noted. The conclusions may be compared with those of the palynologists working in Southern Africa. As I am more familiar with the dry parts of South Africa, examples will chiefly be drawn from that area.

ABERRANT DISTRIBUTIONAL PATTERNS

1. In the eastern Orange Free State and Lesotho, shrubby communities of Afromontane affinity are very common on the stoney slopes of hills and mountains. In the Afromontane zone of Lesotho these communities may occur in continuous belts, but further westward their occurrence is patchy and is interrupted by the extensive grasslands of the Highveld. Still further westwards (around 26° 30′ EL) the grasslands merge into the open dwarf shrub vegetation of the False Karoo which contains species of Karoo-Namib affinity. In this area, patches of scrub vegetation of Afromontane affinity are very rare and of very limited extension. They do occur, however, and are described from steep, sheltered and cool southern slopes in the Upper Orange River area, as Rhamno-Rhoetum scrubland by Werger (1980). They contain species like *Myrsine africana, Rhamnus prinoides, Kiggelaria africana, Celtis africana, Grewia occidentalis,* and many other shrubs, herbs and graminoids abundant in the higher, cooler and wetter parts of southern Africa. The patchy distribution pattern of this vegetation type fading out in a westward direction, the westwardly diminishing abundance and presence of Afromontane species in stands of this community, as well as the ecological characteristics of its habitat (see Werger, 1980), strongly suggest that the present occurrences are remnants from a previously more continuous westward extension of the distribution area of this vegetation type. Such an extension can only have existed under generally wetter and perhaps cooler conditions. Judged from the climatic conditions under which the Afromontane vegetation in the eastern Orange Free State and Lesotho optimally occurs, especially wetter conditions must

have prevailed in order to allow a more continuous westward extension as required for this explanation.

2. The pattern described above is more or less repeated a few hundred kilometres further westward (between 23°30′ and 24° EL), where well within the domain of the Pentzietea incanae communities which are strongly of Karoo-Namib affinity, stands with a clear Sudano-Zambezian affinity occur on sheltered, south-eastern slopes of dolerite. These stands belong to the Zizipho−Rhigozetum obovati association described by Werger (1980). Sudano-Zambezian species occurring in these stands include *Themeda triandra, Digitaria eriantha, Heteropogon contortus, Sansevieria aethiopica* and many others.

This isolated, patchy occurrence of Sudano-Zambezian vegetation islands on sheltered sites within the Karoo-Namib area again suggests a formerly more continuous westward extension of these vegetation types. This again asks for a formerly somewhat wetter climate in that area.

This westward 'penetration' of vegetation types of generally wetter and/or cooler areas into the drier and warmer areas is remarkably reminiscent of the 'distant satellite' distribution pattern of several Afromontane species westwards along watersheds, discussed by White (1978, 1981) as the Zambezi, Limpopo and Magaliesberg extensions.

3. The southern Kalahari represents a marginal savanna area on deep sandy soils. The affinity of its flora is mainly Karoo-Namib, and therefore the area is included within that phytogeographical region (cf. Werger, 1973, 1978a). However, Karoo-Namib species are nearly all species of the fieldlayer (which constitutes by far the most significant part of southern Kalahari vegetation), whereas especially in the very open layer of shrubs and small trees, a number of Sudano-Zambezian species are important. This Sudano-Zambezian group mainly concerns woody species with a relatively deep root system that enables them to draw on the water supplies deeper in the ground. As most of the Karoo-Namib species of the southern Kalahari do not possess such a relatively deep root system, they cannot draw on these moisture resources. This co-occurrence of ecologically and phytogeographically contrasting plant species within the same community, suggests that it is just a temporary stage resulting from a climatic shift: during a previously more humid period the Sudano-Zambezian vegetation types occupied an area which extended much further southwestward, including all or most of the southern Kalahari. With the more recent gradual climatic desiccation the shallow-rooting species of the field layer could not cope with the increasingly severe periodic droughts in the uppermost sandy soil layers and could not maintain themselves. They were replaced by Karoo-Namib species which stand prolonged periods of drought better. The deeper-rooting shrubs and tall trees, however, did not meet this water problem to quite the same extent, since the deeper layers of the sandy soil as yet contain sufficient water under the present rainfall regime. Therefore, these Sudano-Zambezian species were able to maintain themselves in a progressively aridifying area.

Also the marginal woodland communities described from the vicinity of Mafeking by Van der Meulen (1979) and consisting of a similar mixture of species of Karoo-Namib and Sudano-Zambezian affinities, can perhaps best be interpreted in this way.

A similar explanation seems possible for the stands of the Sudano-Zambezian *Colophospermum mopane,* deeply penetrating the northern part of the Karoo-Namib region in South West Africa (Namibia) along dry valleys and islandwise tapering out in a westward direction (Werger & Coetzee, 1978). In this case it is, of course, also possible that the distribution pattern results from regeneration from seeds brought by occasionally flowing rivers in these valleys, though *Colophospermum* cannot be regarded as a fluviatile species. Should this distributional pattern be interpreted as resulting from a previously wetter period, this period cannot be interpreted as having been much colder as well, since *Colophospermum mopane* is very sensitive to low temperatures, its southern boundary coinciding largely with the 5°C isotherm of mean daily minimum temperature for the coldest month (see Henning & White, 1974).

4. The higher parts of the high mountains of the western escarpment in Namaqualand are islands of narrow-leaved sclerophyllous dwarf shrub vegetation in an area generally covered with strongly succulent dwarf shrub vegetation. In physiognomy and floristical composition, this sclerophyllous dwarf shrub vegetation is strongly related to the karroid vegetation of the interior plateau, which experiences summer rainfall and, in an eastward direction, increasingly severe and frequent frosts in the winter season, as well as an increasingly higher annual precipitation. The plants making up the karroid sclerophyllous vegetation on the Namaqualand mountain tops and on the interior plateau are predominantly of the C_3-photosynthetic type, whereas the succulent dwarf shrub vegetation of Namaqualand is extremely rich in plants having the Crassulacean Acid Metabolism (CAM) for photosynthesis (Werger & Ellis, 1981). Massive occurrence of CAM-plants seems to be limited by both a threshold of too low and one of too abundant moisture supply, while on the other hand the moisture supply must be rather regular. Namaqualand with its dry winter rainfall climate and its frequent nightly or early-morning fog and dew, seems to meet these requirements. On the other hand, regular frosts of a certain severity, the suggestion is a lower limit of about −4 or −5°C, seem to prevent the massive occurrence of CAM-plants. It is most likely that the regular occurrence of such low temperatures in the higher parts of the Namaqualand mountains is the main reason why the succulent dwarf shrub vegetation is replaced there by sclerophyllous dwarf shrub vegetation, which is frost-tolerant, even though the general moisture conditions on these higher parts are perhaps favourable for CAM-plants. On the other hand, the more frequently humid conditions in the higher parts of these mountains may also favour the narrow-leaved, sclerophyllous karroid dwarf shrub vegetation there.

A second interesting feature of these sclerophyllous karroid vegetation islands, and one that contrasts strongly with the case to be discussed next, is that apparently there has been relatively little speciation within these islands; there are relatively few endems restricted to single or few mountain tops, and the species composition appears to be rather constant from island to island. In this respect this sclerophyllous dwarf shrub vegetation differs from the fynbos vegetation capping the mountain tops further southwards in the marginal area of the Karoo. In these isolated fynbos islands local endems apparently are more common (cf. Taylor, 1978).

The low-temperature tolerance of the sclerophyllous C_3-dwarf shrubs, their possibly higher moisture demands, and the scarcity of extremely localized endems together point to a recently cooler and perhaps wetter climate in this area under which the sclerophyllous vegetation islands formed a continuous belt, and the succulent vegetation was restricted to considerably lower altitudes than at present.

These cooler and perhaps wetter conditions must have existed until rather recently, otherwise the sclerophyllous vegetation islands would most probably have shown a far higher degree of speciation through isolation.

5. In the same area of Namaqualand discussed above, but in the succulent dwarf shrub vegetation, a number of succulent species show a very remarkable distribution pattern. Though growth conditions for succulent dwarf shrub vegetation seem to be fairly constant over wide stretches of land at lower and middle altitudes, a surprisingly large number of species show a very patchy distribution: one species is restricted to a limited plain or slope, whereas on the adjacent plain or next slope another closely-related, but distinct species takes its place, and there are no identifiable differences in ecological conditions between these sites that would explain such a replacement of species. In fact, the distribution areas of these closely-related species often are not even interrupted by ecologically different sites but form one homogeneous habitat area. This patchy distribution is especially frequent within the Mesembryanthemaceae, though it seems not to be restricted to it; with closer study it probably will also be found in the Portulacaceae, Crassulaceae, Liliaceae and Euphorbiaceae. Several examples are now known from the mesembryanthemaceous genera *Mitrophyllum, Psilocaulon, Aridaria,* etc. and gradually more cases of this phenomenon come to light through the thorough investigations of prof. Ihlenfeldt and his co-workers into this family. Hartmann (1977), for example, reported a very similar distribution pattern for the species of the mesembryanthemaceous genus *Argyroderma* in the quartzitic Knersvlakte in southern Namaqualand. This type of patchy distribution resembles the pattern of highly localized endems in the area of the Cape fynbos vegetation. It is a kind of distribution that creates high γ-diversities in the sense of Whittaker (1977).

A plausible explanation for this patchy and localized distribution pattern of some closely-related, but distant species of succulents in an area that often appears as homogeneously 'suitable' for each of the species, is that it again results from a previously decidedly cooler and perhaps wetter climate. Under such a climate frosts will have been more severe and more frequent, and conditions will have been generally more humid, both favouring the sclerophyllous vegetation now concentrated on the higher parts. Such conditions diminished the habitat suitable for the succulent dwarf shrub vegetation to a few favourable sites, which, limited in size, protected them against the coldest temperatures by their exposition, their exposure to mild sea winds, and their low elevation. In these isolated favourable sites, selection pressures must have worked effectively on a rather small gene pool, with the result that in some cases distinct species evolved parapatrically in each or several of these islands. This process of speciation so far resembles the evolution by biotype depletion assumed by Wild (1965) for many endems of the serpentine soils of the Great Dyke in Zimbabwe (see also literature cited in Goldblatt, 1978: 410). Keeping in mind the ecophysiological requirements of the Namaqua succulents, the climate, though cooler, must have been a winter rainfall climate, with a regular, but not too high moisture supply [see above under (4)]. When the climate became warmer and drier, the area suitable for these succulents extended and the isolated patches expanded, enlarging into a continuous stretch of favourable land, only locally interrupted by unfavourable mountain tops. With the expansion of the suitable habitat, the distribution areas of the succulents increased and met each other.

In several cases, where small, isolated populations had not evolved into distinct species, the isolation was removed and an exchange of genetic material into one larger and genetically more diverse population must have resulted. Where distinct species had evolved, however, newly interconnected island-areas could either exchange their species or, when these species are ecologically similar, upon immigration, they could have outcompeted one another in some of the previously isolated areas. Of this latter phenomenon there is little evidence in Namaqualand, since in several cases closely-related but distinct species occur in 'pure areas' within short distances from one another, without much immigration or overlap of distribution areas being noticeable. Even when keeping in mind that antitelechoric devices are common in plants of arid regions, and thus also in the Namaqua flora (Stopp, 1958, Werger, 1978a), this apparent lack of mutual penetration into the distribution areas of the previously isolated species strongly suggests that the change from a cooler to a warmer climate must have occurred relatively recently.

COMPARISON WITH OTHER PALAEOCLIMATIC FINDINGS

The conclusions from the cases discussed above is that the aberrant distributional patterns in a considerable number of vegetation types point to a recently wetter and cooler climate over much of South Africa, and certainly in the central, western and southern parts. In at least the central parts it appears that the higher humidity was all-important, whereas on the western escarpment the lower temperatures possibly may have been of equal or more importance than the increased humidity.

Though the anomalies discussed here allow these conclusions, they cannot be dated so that they do not allow a clear conclusion on whether or not change in climate occurred everywhere at the same time, and to a very limited extent only on whether or not such a climatic change occurred once or repeatedly.

All palynologists agree that, since the Pleistocene, there have been repeated changes of climate that have been of different magnitude. Geomorphologists agree with this finding (e.g. Harper, 1969; Street & Grove, 1976; Heine, 1978, 1979). Van Zinderen Bakker (1975, 1978) states that at present we are in the second half of an interglacial. During a glacial period the presently tropical parts north of South Africa received much less rainfall and were cooler than at present, wheras the latitudes at which South Africa is situated were wetter and cooler as the winter rainfall area extended further northward and further inland. Coetzee (1978a, b) describes these changes in temperature, precipitation and seasonality as a result of pendulating shifts in climatic regimes during the Quaternary, and gives evidence from various disciplines. Though results also definitely point to a previously cooler and wetter climate, evidence has not been found of a predominantly winter rainfall regime during that period. But, except for the more westward extension of the Sudano-Zambezian element into the dry areas, no evidence was found to the contrary either. The limited evidence available from pollen data from South Africa indicates that there was a definite change in climate from rather dry and warm to more humid and cool around 25 000 B.P., whereas other pollen diagrams have shown repeated alternations from wet–cool to dry–warm conditions between about 13 000 and 10 000 B.P. (Van Zinderen Bakker, 1978; Coetzee, 1967, 1978a, b). Geomorphological evidence (Heine, 1978, 1979, 1981) showed that in the southern Kalahari the time-span from 18 000 to 13 000 B.P. was cool and sometimes wet, sometimes dry with spatially strongly different conditions. Around 30 000 B.P. it probably was wet, and the data indicate that this wet period probably lasted till at least 25 000 B.P. As the southern Kalahari often fell in the transition area of the winter and summer rainfall regimes during the Quaternary, the data are difficult to interpret. More recent alternations of such climatically contrasting spells have been reported (e.g. Frenzel in Van Zinderen Bakker, 1969; Street & Grove, 1976; Heine, 1981). It is, therefore, likely that the patterns discussed here result from different periods of wet and cooler climate, especially since, for example, case (3) probably indicates a less drastic climatic change than that required to result in the pattern of cases (4) and (5). The palynological and geomorphological evidence suggests, however, that the patterns discussed here are of a more recent origin than the arid disjunctions across Africa reported extensively elsewhere (see e.g. Werger, 1978a). It should be stressed that the most important result from the investigation presented here, is that the conclusions independently arrived at by a logical analysis of present vegetation geographical anomalies are not at variance with the palaeoclimatic findings of palynologists and geomorphologists, but seem to confirm them.

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Flore et végétation actuelles de l'Afrique du nord, leur signification en fonction de l'origine, de l'évolution et des migrations des flores et structures de végétation passées

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RÉSUMÉ

A la lumière des travaux et synthèses biogéographiques récentes, la flore méditerranéenne apparaît de plus en plus comme un ensemble hétérogène, reflétant en grande partie l'histoire paléogéographique et paléoclimatique de la région. En particulier la coexistence d'éléments de souche méridionale et d'éléments plutôt septentrionaux, traduit actuellement encore les possibilités d'échanges survenues très tôt au Tertiaire entre les flores de type gondwanien ou du moins tropical et les flores Laurasiennes.

Les éléments tropicaux sont nombreux et peuvent se rattacher à divers ensembles suivant leur âge; un ensemble pantropical réunissant en particulier *Tetraclinis, Warionia,* mais aussi diverses familles, est commun à toutes les régions tropicales et sans doute contemporain de la dislocation du Gondwana; un ensemble nord-tropical singulièrement commun à la Californie et à la région méditerranéenne; un ensemble paléotropical lui-même fort hétérogène et complexe. On y retrouve:

- — des types sclérophylles thermophiles souvent liés à des espèces de la forêt pluviale africaine,
- — des types xérophiles anciens, distribués en Afrique du Sud et au Nord de l'Equateur (randflora),
- — des taxa endémiques des hautes montagnes africaines, affines d'espèces d'Ethiopie ou des hautes montagnes africaines.
- — des taxa d'immigration plus récente voire des espèces saheliennes banales mises en place au cours du dernier pluvial.

Les éléments de souche extratropicale sont composés d'éléments autochtones ou méditerranéo-tertiaires, et d'éléments septentrionaux. Les éléments méditerranéo-tertiaires sont les vestiges des flores différenciées en général 'in situ' sur les rives de la Tethys et sur les microplaques qui y sont apparues. Le rôle de la microplaque ibérique est en particulier capital au Maghreb occidental. Il convient d'en rapprocher diverses espèces appartenant à des souches Irano-touraniennes et Saharo-Arabe, dont la mise en place est souvent récente. Un ensemble oro-mésogéen est particulièrement important et rassemble des taxa endémo-vicariants présents en général de l'Atlas à l'Himalaya occidental. Les éléments septentrionaux réunissent un ensemble mésotherme, vestige des flores Laurasiennes préglaciaires, très mal représenté en Afrique du Nord, un ensemble septentrional microtherme groupant en général des espèces à mise en place récente et un ensemble buréo-alpin contemporain des dernières glaciations, extrèmement localisé sur les hautes montagnes atlasiques.

Enfin, l'origine des principales formations caractéristiques des divers étages méditerranéens est envisagée et discutée.

ABSTRACT

PRESENT VEGETATION AND FLORA OF NORTHERN AFRICA, THEIR MEANING IN RELATION TO THEIR ORIGIN, EVOLUTION AND MIGRATIONS OF FLORAS AND THE STRUCTURES OF PAST VEGETATION

In the light of recent works and biogeographic synthesis, the Mediterranean flora appears more and more as a heterogeneous entity, reflecting, to a great extent, the palaeogeographic and palaeoclimatic history of the region. In particular, the co-existence of elements of southern stock and of northerly elements, presently points to the possibilities of exchange which occurred very early in the Tertiary between the Gondwanian type of floras or the less tropical types and the Laurasian floras.

The tropical elements are numerous and can be linked to various entities according to their age; a pantropical entity comprising in particular, Tetraclinis *and* Warionia, *but also various families, is common to all the tropical regions and, without any doubt, contemporary with the dismemberment of Gondwana; a north-tropical entity peculiarly common to California and the Mediterranean region; a palaeotropical entity strongly heterogeneous and complex. One finds there:*

- *— thermophilous sclerophyll types often linked to the African rainforest species,*
- *— old xerophilous types, distributed in South Africa and north of the Equator (randflora),*
- *— endemic taxa of high African mountains, showing affinities with Ethiopian species or of the high African mountains,*
- *— taxa more recently arrived or even common sahelian species settled during the last pluvial.*

The elements of extratropical stock are composed of autochthonal or Mediterraneo-Tertiary elements, and of northern elements. The Mediterraneo-Tertiary elements are the remnants of differentiated floras generally in situ *on the banks of the Tethys and on the micro-plates which occur there. The role of the Iberian micro-plate is particularly important in the western Magreb. It is advisable to associate them with various species belonging to the Irano-touranian and Saharo-Arab stocks, whose settlement is often recent. An oro-Mesogean entity is particularly important and brings together the endemo-vicariant taxa generally occurring from the Atlas to the western Himalayas. The northern elements bring together a mesothermal entity, a remnant of the pre-glacial Lauresian floras, poorly represented in north Africa, a microthermal northern entity generally comprising species recently established and a north-alpine entity contemporary with the last glaciations, extremely localized on the high Atlas mountains.*

Finally, the origin of the main characteristic formations of the Mediterranean stages is examined and discussed.

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Il peut paraître irréaliste d'envisager en quelques pages la signification des flores et végétations de l'Afrique septentrionale en fonction de leurs origines, de leur évolution et des migrations qu'elles ont pu subir. En fait, nous nous contenterons d'évoquer ici quelques problèmes généraux, renvoyant le lecteur à d'autres travaux récents (Walter & Straka, 1970; Axelrod, 1973; Raven, 1972–1973; Axelrod & Raven, 1978; Quézel, 1978; Quézel, Gamisans & Gruber, 1980). Nous n'aborderons pas les problèmes historiques et paléobotaniques évoqués par ailleurs, sauf lorsqu'ils apparaîtront indispensables à la compréhension du texte.

L'Afrique septentrionale (Afrique méditerranéenne et saharienne) représente à l'heure actuelle la partie de ce continent où la diversité écologique et biogéographique est de loin la plus importante. En particulier, les modifications survenues depuis la fin du Miocène, tant au niveau des climats que dans la composition des flores n'ont sans doute, nulle part dans le monde, été aussi drastiques. Ces transformations ont déterminé le déferlement de flores extrêmement hétérogènes, tropicales et extratropicales, dont les vestiges actuellement en place posent d'immenses problèmes. Les interprétations proposées ci-dessous restent en partie hypothétiques, mais elles ont au moins le mérite de situer le problème et de constituer une base de discussion.

L'Afrique septentrionale s'intègre dans le même schéma que l'ensemble du monde méditerranéen; elle s'en distingue toutefois surtout par l'existence d'une gamme de climats extrêmement diversifiée, où les types xériques et thermiques accentués sont largement représentés (Daget, 1977), et par une continuité, théorique au moins, avec le monde paléotropical. Rappelons qu'elle se situe sur la charnière historique entre la Laurasie et le bloc africain partie intégrante du Gondwana, et que la microplaque ibérique (Biju-Duval, 1976) a servi de trait d'union de façon quasi ininterrompue entre ces deux grands ensembles. Cette dualité est encore aujourd'hui évidente au niveau de la flore mais également des structures de végétation.

1 LES ÉLÉMENTS DE SOUCHE MÉRIDIONALE

Leur importance dans la flore actuelle de l'Afrique septentrionale est plus grande qu'on ne le pensait il y a encore quelques décennies (Raven, 1972–1973; Quézel, 1978; Quézel, Gamisans & Gruber, 1981), mais leur interprétation historique et biogéographique n'est pas toujours aisée. Il est possible de distinguer divers ensembles:

1.1 *L'ensemble pantropical*

Il réunit un nombre appréciable de taxons ou de familles, de répartition actuelle fortement disjointe, mais présents sur l'ensemble des territoires tropicaux. Sa mise en place, doit être considérée comme antérieure à la dislocation du bloc continental méridional (Crétacé inférieur ou moyen). Les cas les plus significatifs en Afrique du Nord sont ceux des genres *Tetraclinis,* bien proche des *Callitris* australiens, ou *Warionia,* seul représentant méditerranéen des Astéracées — Mutisiées. En fait, un nombre non négligeable de genres peut être intégré à ce groupe; c'est le cas pour les suivants: *Aristolochia, Acacia, Celtis, Coriaria, Ficus, Ilex, Maytenus, Myrtus, Osyris, Prosopis, Vitis, Tamarix, Ziziphus.*

1.2 *L'ensemble nord-tropical*

Quoique plus récent, il reste hautement significatif, puisqu'il réunit des genres de souche méridionale, actuellement présents à la fois en Afrique du Nord et en Amérique nord-occidentale, Californie surtout (Axelrod & Raven, 1978; Quézel, 1978), dont la mise en place, antérieure à la formation de l'Atlantique nord, doit donc remonter à l'Eocène. Citons les genres: *Boerhavia, Cleome, Commicarpus, Fagonia, Lycium, Pistacia, Rhus, Smilax, Talinum, Trianthema, Vitex.*

1.3 *L'ensemble paléo-tropical*

C'est de loin le plus important et le plus complexe; il doit être subdivisé en plusieurs groupes.

1.3.1 Un lot très remarquable est constitué par des taxons sclérophylles jouant actuellement un rôle considérable en région méditerranéenne, en particulier dans la constitution des structures de végétation de l'étage thermo-méditerranéen (Quézel, 1974; Ozenda, 1975). Ils y sont le plus souvent représentés par des espèces particulières, voire par des genres endémiques, en place au moins depuis le Miocène (Suc, 1980). Tel est le cas pour les représentants des genres *Asparagus, Capparis, Ceratonia, Chamaerops, Jasminum, Laurus, Olea, Nerium, Phillyrea, Viburnum.* Divers représentants de la laurisylve canarienne, disparus d'Afrique du Nord, entrent également dans ce lot: *Apollonias, Myrsine, Ocotea, Persea, Visnea.*

1.3.2 Un groupe important de taxa xérophiles de souche indiscutablement africaine est à signaler ici. Il est en général rapporté à l'élément érémitique africain ou 'randflora' (Aubréville, 1949; Monod, 1951; Quézel, 1958) et donne lieu à de multiples disjonctions nord-sud tropicales en Afrique. Son individualisation ne semble pas pouvoir être antérieure à des phases franchement arides qu'il est difficile de repérer en amont de la fin du Miocène (Messinien en particulier); son extension a été au moins en partie assurée au cours des épisodes xériques plio-pleistocènes. De très nombreux représentants existent en Afrique du Nord méditerranéenne et au Sahara (*Amphinomia, Andrachne, Aristida (p.p.), Caralluma, Enneapogon, Gaillonia, Oropetium, Periploca, Tribulus, Trichodesma, Zygophyllum).* Il convient également de rattacher à ce groupe, divers taxons xérophiles en général présents aux Canaries (y compris le secteur macaronésien marocain) mais aussi souvent sur les rives de la Mer Rouge, voire parfois sur les hautes montagnes sahariennes. C'est le cas pour les *Euphorbia* cactoïdes, mais aussi pour divers représentants des genres *Acacia, Ceropegia, Commelina, Dracaena, Kalanchoe, Kleinia, Mesembryanthemum, Pentzia, Wahlenbergia.* L'endémisme est ici très généralement spécifique, exceptionnellement générique (*Argania*), ce qui paraît bien correspondre aux hypothèses énoncées plus haut quant à l'ancienneté de cette unité.

1.3.3 Une mention spéciale doit être faite pour diverses espèces des massifs montagneux sud et centro-sahariens, dont les affinités sont à rechercher auprès d'éléments montagnards africains, voire afro-alpins, présents sur la dorsale africaine et en particulier en Ethiopie et au Jebel Marra (Quezel, 1965). Leur mise en place qui ne saurait être antérieure à la surrection de cette chaîne volcanique, soit au début du Miocène (Axelrod & Raven, 1978), s'est poursuivie épisodiquement jusqu'à des dates récentes (Hedberg, 1965) et en particulier durant les pluviaux pleistocènes. La présence à ce niveau de taxa endémiques diversifiés avec types endémo-vicariants (*Rhynchosia, Pentas, Phagnalon, Helichrysum, Dichrocephala, Albuca, Kosteletzkia*) à côté de types simplement disjoints (*Eleocharis intricata, Dicoma capensis, Erhetia obtusifolia, Hermannia abyssinica*) paraît le confirmer. Rappelons d'ailleurs que c'est au moins en partie par cette voie qu'ont pu s'effectuer des échanges entre les flores du Cap et celles de la région méditerranéenne, comme le confirme très clairement la répartition des *Erica* du groupe *Erica arborea* (Bruneau de Miré & Quézel, 1959) et l'existence entre ces deux régions d'un nombre appréciable de couples génériques vicariants (Burtt, 1971; Goldblatt, 1978). Cette voie de migration a d'ailleurs fonctionné dans les deux sens, ce qui permet d'expliquer également la présence sur les hautes montagnes africaines d'éléments de souche mésogéenne, voire européenne (Hedberg, 1965).

1.3.4. Enfin, l'existence de phases pluviales africaines récentes, dont la dernière ne saurait remonter au delà de quelques millénaires (Quézel & Martinez, 1961), a largement permis l'invasion des vallées sahariennes par une flore sahélienne typique et qui n'a pas eu le temps d'évoluer, notamment sur les revers sud-occidentaux du Hoggar et du Tibesti (Quézel, 1965) où elle réunit près de 250 espèces. Certains de ces éléments ont atteint largement la région méditerranéenne, mais sans doute déjà plus anciennement pour plusieurs d'entre eux comme notamment les Andropogonées (Quézel, 1958), ou au contraire très récemment et peut-être par ornithochorie ou anthropochorie, en particulier pour diverses espèces hygrophiles et aquatiques, *Fimbristylis, Fuirena, Oldenlandia, Laurembergia*, ou encore culturales, *Echinochloa, Panicum, Eragrostis*.

2 LES ÉLÉMENTS DE SOUCHE EXTRA-TROPICALE

Ils représentent le lot le plus important dans la flore de l'Afrique septentrionale. On peut y distinguer deux groupes principaux, l'un réunissant les éléments autochtones, l'autre plus spécifiquement septentrional ou holarctique; leur distinction n'est pas toujours aisée.

2.1 *Le complexe autochtone ou mésogéen*

Diversifié sur les rives de la Mésogée tertiaire, cette unité peut être subdivisée à son tour en plusieurs ensembles (Quézel, 1978), en particulier, un ensemble autochtone ou méditerranéo-tertiaire, un ensemble irano-touranien et un ensemble saharo-arabe; nous envisagerons aussi séparément l'ensemble oromésogéen.

2.1.1 *L'ensemble autochtone ou méditerranéo-tertiaire*

L'Afrique septentrionale n'est ici qu'un cas particulier du monde méditerranéen. Comme nous l'écrivions récemment (Quézel, Gamisans & Gruber, 1980), la richesse actuelle de la région méditerranéenne et le haut niveau d'endémisme qui s'y observe paraissent être la preuve de l'individualisation 'in situ' de très nombreux taxons. Le problème majeur est que ceux-ci sont actuellement liés à un type climatique très particulier dont la mise en place progressive et intermittente (Suc 1980a) ne saurait remonter, du moins dans l'état actuel de nos connaissances, au delà du Miocène terminal, Messinien en particulier. Toutefois, très curieusement, l'existence d'un lot appréciable de taxons vicariants (à l'échelon spécifique) entre les régions climatiquement méditerranéennes de l'Ancien et du Nouveau Monde septentrionaux pose question. A moins d'admettre une singulière adaptation écologique parallèle, la présence en Méditerranée et en Californie de représentants des genres *Arbutus, Berberis, Helianthemum, Lavatera, Salvia, Cupressus* ou encore de *Quercus* sclérophylles, ne peut être expliquée que par une mise en place probablement Eocène (Axelrod, 1973; Axelrod & Raven, 1978; Quézel, 1978) et de toute façon antérieure à l'apparition définitive de l'Atlantique Nord. La région circum-méditerranéenne malgré son extrême richesse floristique et en endémiques, ne possède toutefois aucune famille particulière, alors que la région méditerranéenne du Cap, territorialement fort exiguë, en offre au moins 6 (Goldblatt, 1978).

Si les éléments de souche méditerranéenne en Afrique septentrionale représentent le contingent le plus important, leur richesse et en particulier leur richesse en endémiques varie considérablement suivant les régions. C'est ainsi (Quézel, Gamisans & Gruber, 1980), qu'une partie importante du Maghreb occidental correspond au moins à une partie des vestiges de la microplaque ibérique (cf. supra), ce qui explique le haut niveau d'endémisme présenté par cette région (26 genres endémiques sur les 38 existant dans les 3 pays de l'Afrique du Nord y sont présents ou localisés, plus une douzaine de genres strictement ibéro-marocains). Cette richesse contraste avec la relative homogénéité floristique des autres portions de l'Afrique septentrionale méditerranéenne, sauf toutefois, mais à bien moindre titre, le secteur macaronésien marocain (*Hannonia, Sclerosciadium, Traganopsis*) mais aussi la Cyrénaïque (*Pachyctenium, Libyella, Euhesperida).*

2.1.2 *L'ensemble Irano-Touranien*

Le développement d'une flore essentiellement steppique liée à un climat fortement contrasté mais toujours de type mésogéen est un phénomène dont l'origine reste encore mal connue. C'est sans doute sur le revers septentrional de la Mésogée orientale (Quézel, Gamisans & Gruber, 1980) qu'elle s'est indivudialisée à la faveur des phases sèches et froides, épisodiques au moins depuis la fin du Miocène, comme le montre sa richesse en éléments endémiques. Cette flore est actuellement assez mal représentée en Afrique septentrionale (une quarantaine de taxa avec de rares espèces endémiques), ce qui paraît plaider en faveur d'une immigration récente et sans doute contemporaine des épisodes pleni- et post-glaciaires quaternaires, périodes correspondant à l'extension des flores polliniques à *Artemisia, Ephedra,* Chénopodiacées et *Juniperus* sur le pourtour méditerranéen occidental (Bazile-Robert, Suc & Vernet, 1980; Quézel, Barbero, Bonin & Loisel, 1980). Son rôle dans l'individualisation de la flore oro-mésogéenne est également à rappeler (cf. infra).

2.1.3 *L'ensemble Saharo-Arabe*

L'installation des vastes zones désertiques au sud de la région méditerranéenne, ne saurait être antérieure à la charnière mio-pliocène comme le montrent les données géomorphologiques (Butzer & Hansen, 1968; Rognon, 1976) et palynologiques (Maley, 1980); encore a-t-elle été progressive et intermittente et il apparaît que la situation actuelle est la pire connue par ces régions. La flore correspondante (Quézel, 1978) s'est constituée à partir des éléments les plus xérophiles appartenant aux éléments floristiques voisins, ce qui a en particulier permis l'extension de la 'randflora' africaine, mais aussi de nombreux éléments de souche mésogéenne où l'endémisme dépasse rarement l'échelon spécifique, sauf sur les marges sahariennes nord-occidentales climatiquement moins hostiles, où sont présents, mais pas toujours localisés, 14 des 15 genres endémiques du Sahara.

2.1.4 *L'ensemble oro-mésogéen*

La surrection de hautes chaînes, de l'Atlas à l'Himalaya, surrection qui s'est poursuivie durant le Pliocène, voire le Pléistocène, a déterminé, l'individualisation de flores particulières, dont l'histoire est complexe. Cette flore orophile s'est constituée d'éléments autochtones, mais a bénéficié d'importants apports à l'occasion des périodes glaciaires. L'ensemble oro-mésogéen est formé d'un fond floristique commun avec apparition de nombreux phénomènes d'endémo-vicariance particulièrement perceptible sur les chaînes actuellement soumises à un climat méditerranéen (Atlas — Taurus — Liban — Himalaya occidental). Nous en avons indiqué de nombreux exemples (Quézel, 1957-1978) et notamment ceux des genres *Abies, Asperula, Berberis, Cedrus, Cotoneaster, Cerasus, Dracocephalum, Juniperus, Lonicera, Papaver, Silene,* etc. Pour des raisons climatiques mais aussi biogéographiques, c'est au niveau de cette flore que divers taxa plus spécifiquement Irano-Touraniens ont pu persister: *Artemisia, Astragalus, Scutellaria, Onosma.* Bien évidemment la flore autochtone planitiaire a fourni de nombreux éléments, mais il faut signaler l'absence de genres endémiques orophiles, du moins sur les monts Atlas, alors que l'endémisme spécifique y atteint environ 25%. Sa mise en place préglaciaire est évidente.

2.2 *Le complexe septentrional*

Il réunit divers ensembles de valeur historique et biogéographique très différente, individualisés sur le bloc Laurasien et échappant aujourd'hui aux contraintes climatiques méditerranéennes.

2.2.1 *L'ensemble septentrional mésotherme*

Nous réunissons dans ce groupe (Quézel, Gamisans & Gruber, 1980) une flore caractéristique de climats perhumides tempérés voire tempérés chauds, de souche Laurasienne évidente, qui a joué un rôle de premier plan dans la constitution des flores préglaciaires dans toute la région méditerranéenne et en Afrique du Nord, notamment au Pliocène (Arambourg, Arènes & Depape, 1953; Van Campo *et al,* 1965–1968; Axelrod, 1973).

Les familles suivantes sont en particulier à citer: Taxodiacées, Juglandacées, Hammamélidacées, Platanacées. Si cet élément, qui a fort mal supporté les modifications climatiques pléistocènes, a pratiquement disparu du Maghreb, il y a toutefois laissé quelques vestiges *Epimedium, Laurocerasus, Paeonia* et *Chrysosplenium dubium.*

2.2.2 *L'ensemble septentrional microtherme*

Il est constitué par des taxa essentiellement liés, en Afrique septentrionale, aux milieux humides et montagnards. Son arrivée est en grande partie contemporaine des phases pluviales quaternaires et on peut lui rapporter divers représentants des genres *Acer, Fraxinus, Tilia, Ulmus* et de nombreux éléments herbacés (Quézel, 1978); l'endémisme y est absent ou atteint tout au plus le niveau subspécifique. Toutefois la présence dans la flore orophile atlasique d'endémiques de haut niveau (sections) dans les genres *Gentiana* et *Draba* doit faire envisager les possibilités d'une origine plus ancienne. L'existence au Tibesti (Quézel, 1958) de quelques éléments endémiques pouvant s'y rattacher (*Asplenium quezelii, Helosciadium muratianum,* etc.) pose d'ailleurs le même problème.

2.2.3 *Les éléments boréo-alpins*

La découverte (Maire, 1924) sur les sommets du Haut Atlas d'espèces et de structures de végétation d'affinité boréo-alpine a été une immense surprise. Rappelons simplement ici qu'une vingtaine de taxons boréo-alpins et une quinzaine d'éléments orophiles européens (Quézel, 1957) y ont été recensés. Leur mise en place est certainement contemporaine des grandes phases glaciaires quaternaires, comme semble le prouver l'absence quasi complète d'endémisme.

3 LES STRUCTURES DE VÉGÉTATION

L'analyse des structures actuelles de végétation en Afrique septentrionale est susceptible de fournir de précieux renseignements sur leur signification historique. Elle confirme en grande partie les conclusions auxquelles conduit l'étude de la flore. Nous avons déjà largement abordé cette question (Quézel, 1978), mais quelques points particuliers méritent toutefois d'être précisés. En effet, les interprétations biogéographiques fournies ci-dessus, ont été établies en fonction de l'origine historique des taxons. Actuellement, ces divers ensembles et spécialement les plus anciens, sont confondus au niveau des grandes structures de végétation imposées par le climat. Si l'on s'en tient aux critères physionomiques (Quézel, 1974), quelques faits restent cependant à souligner.

- — à l'étage thermoméditerranéen, les essences dominantes sont pratiquement toutes des éléments anciens de souche méridionale et à feuilles sempervirentes (*Ceratonia, Chamaerops, Maytenus, Myrtus, Olea, Nerium, Pistacia, Rhus, Tetraclinis,* etc..).
- — à l'étage mésoméditerranéen dominent au contraire les éléments sclérophylles autochtones (*Arbutus, Cupressus, Quercus*), sans que les lignées méridionales n'aient totalement disparu *(Jasminum, Phillyrea, Viburnum).*
- — au contraire, à l'étage supraméditerranéen, la végétation de type caducifolié accuse une origine septentrionale (Chênes caducifoliés, *Acer, Fraxinus, Tilia, Ulmus,* etc..).
- — la végétation de l'étage montagnard méditerranéen est presqu'exclusivement constituée par des éléments autochtones (Sapins méditerranéens, *Cedrus, Juniperus* arborescents, *Pinus* spp.).
- — enfin, à l'étage oroméditerranéen, la végétation est encore essentiellement de souche autochtone, enrichie d'éléments Irano-Touraniens en ambiance xérique, voire d'éléments septentrionaux en ambiance hygrophile.

Pour des raisons écologiques évidentes, la flore Saharo-Arabe reste liée au climat saharien, alors que les influences Irano-Touraniennes sont perceptibles surtout en climat aride (steppique) froid.

Quelques précisions peuvent encore être ajoutées: ainsi, la 'randflora' présente au Sahara devient dominante à l'étage inframéditerranéen défini essentiellement par les *Euphorbia* cactoïdes et présents aux Canaries et au Maroc sud-occidental, sous un climat aride chaud, à humidité atmosphérique élevée. La laurisilve, structure de végétation largement représentée en région méditerranéenne au Mio-Pliocène (Roiron, 1979; Suc, 1980; Bessedik, 1981), a pratiquement disparu du continent africain[*] à la suite des cataclysmes climatiques quaternaires. Elle a persisté par contre aux Canaries, où elle reste liée à un climat humide chaud à nébulosité élevée. Pour les mêmes raisons, l'ensemble septentrional mésotherme a été lui aussi presque totalement éliminé du Maghreb.

Il est intéressant d'évoquer en conclusion, l'exemple fourni actuellement par les Canaries, où les contraintes climatiques ont peu varié depuis le Pliocène. Ces îles océaniques, dont le peuplement n'a pu s'effectuer que par transport hydrochore ou zoochore de diaspores, permettent en effet de retracer de façon synthétique l'histoire du peuplement végétal de l'Afrique du Nord. Les grands ensembles biogéographiques, malgré l'exiguïté du territoire, sont particulièrement aisés à appréhender et déterminent même des paysages très spécifiques en fonction des critères bioclimatiques. Il ne faut pas oublier cependant que ce type de colonisation n'a pas permis le transport efficace sur ces îles de graines lourdes ou fragiles (Cupulifères et Juglandacées en particulier).

En ambiance thermique (m, Emberger, 1930 > 5°C) apparaissent, en fonction des précipitations ou plus exactement du bilan hydrique, des structures de végétation fort différentes:

- — sous climat humide c'est la laurisilve, reflet au moins partiel de la forêt thermo-hygrophile méditerranéenne Mio-Pliocène.
- — sous climat semi-aride ce sont des formations de type thermoméditerranéen typique (brousse à *Olea-Lentiscus).*
- — sous climat aride s'installe au contraire une végétation de type africain, où dominent largement, du moins du point de vue physionomique, les représentants de la 'randflora'.
- — sous climat désertique enfin, sur les îles orientales, apparaît une végétation de type Saharo-Arabe.

En ambiance fraiche voire tempérée (0°C>m<5°C), la végétation est celle d'un étage mésoméditerranéen sub-humide (*Pinus canarienis* avec en sous-bois matorrals à *Adenocarpus, Cistus, Sideritis, Teline,* etc.).

En ambiance froide et très froide (m<0°C), la végétation supraforestière trouve surtout des affinités avec la flore orophile atlasique de type semi-aride à Génistées arbustives.

Soulignons en terminant que si ce schéma reste significatif dans ses grandes lignes, il ne tient pas compte des phénomènes intenses de spéciation qui se sont manifestés sur ces îles et qui en ont singuliérement accru l'individualité floristique.

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[*] *Laurus azoricus* vient toutefois d'être trouvé dans l'Atlas de Ksiba au Maroc (Barbero, Benabid, Peyre & Quézel, 1980).

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Aspects of the phytogeography of African Pteridophyta

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ABSTRACT

A diversity of distribution patterns exhibited by African pteridophytes on intercontinental and continental scales are presented. Occasional random dispersal among the Pteridophyta over long distances is accepted. The ecological importance of the gametophyte phase is inferred. Future progress in the elucidation of African fern phytogeography will require a broader alpha-taxonomic pan-African base and the plotting of many more distribution maps.

RÉSUMÉ

ASPECTS DE LA PHYTOGÉOGRAPHIE DES PTÉRIDOPHYTES AFRICAINS

Une diversité de modes de distribution montrée par les ptéridophytes africains sur des échelles intercontinentales et continentales est présentée. Une dispersion occasionnelle due au hasard parmi les Ptéridophytes sur de longues distances est acceptée. L'importance écologique de la phase gamétophyte est présumée. Les progrès à réaliser dans la connaissance de la phytogéographie des fougères africaines nécessiteront une base pan-africaine alpha-taxonomique plus vaste ainsi que l'établissement de beaucoup plus de cartes de distribution.

INTRODUCTION

Although the spores of pteridophytes are small in comparison to the seeds of most angiosperms and could be liable to widespread dispersal by wind, many African pteridophytes exhibit distribution patterns similar to those of some African angiosperms. As in angiosperms there are endemic species in various habitats and in various regions. At the other extreme there are pantropic fern species as well as those occurring in two continents.

Phytogeographic concepts are immediately suspect unless there are sound taxonomic data bases. There are few critical world wide revisions of pteridophyte genera; consequently the data presented and used in this paper has been investigated and evaluated by the author.

DISTRIBUTION PATTERNS OF SOME WORLD-WIDE SPECIES COMPLEXES

Dryopteris wallichiana is a large and conspicuous fern confined to mountain habitats in many parts of the world. It has a distribution ranging through the Himalayas and high mountains of Sri Lanka, south east Asia, the Hawaiian islands and the mountains of central America and along the Andes. In the African region, it is only known from Inyangani Mountain in Zimbabwe in the shade of *Widdringtonia* sp. and the highest mountain in Madagascar; it is absent from the high mountains of east tropical Africa.

A different distribution pattern is exhibited by the predominantly temperate *Asplenium trichomanes* complex. It is widely distributed in temperate south America, Europe, eastern Asia, South Africa and temperate Australia; it is apparently absent from temperate South America and the east tropical African mountains. Yet another pattern is shown by the *Hymenophyllum tunbridgense* complex, which is apparently absent from North America and Asia.

One even more puzzling distribution pattern is that exhibited by the *Polypodium vulgare* complex which is widely distributed in the northern hemisphere but which is only represented in the southern hemisphere in South Africa and on Kerguelen Island in the Indian Ocean. Other species, such as *Doryopteris concolor*, are virtually confined to the southern hemisphere.

SOME OTHER INTERCONTINENTAL DISTRIBUTION PATTERNS

The *Polypodium polypodioides* complex is widespread in the Americas and is represented in south and east Africa by *P. polypodioides* subsp. *ecklonii. Asplenium platyneuron* exhibits a similar but more restricted range in eastern North America and South Africa. *Woodsia montevidensis* which is widespread in South America is confined in Africa to the Natal Drakensberg. Conversely, *Cyathea capensis*, which is widespread in southern Africa, is restricted in South America to a small area in south eastern Brazil. Among the strictly tropical species common to the Americas and Africa, it is interesting to note comparable wide variation in frond dissection in the South American and west African populations of *Ctenitis protensa*.

A number of African fern species also occur in Asia. Some, such as *Nephrolepis acutifolia* and *Lindsaea odorata*, are widespread in south east Asia but are only known from a few localities in tropical Africa and the Mascarene Islands. Others can be regarded as African species with outliers in Asia; an example is *Pellaea angulosa* from East Africa and the Mascarenes which also occurs in Sri Lanka and the southern tip of India.

Among the more temperate South African ferns, *Todea barbara* is represented by a possibly distinct subspecies in south eastern Australia and New Zealand. At even more southerly latitudes, the cold temperate, south circumpolar *Grammitis poeppigiana* only occurs on the African continent on two high mountain summits near its south western extremity.

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The world-wide distribution of many of the species still needs to be plotted, after critical taxonomic evaluation, before clear trends in patterns can be expected to emerge. However, it is apparent from the available evidence that there is more diversity in distribution patterns among the pteridophytes than one would initially expect in a group with presumably wind-dispersed spores.

DISTRIBUTION PATTERNS OF FERNS IN AFRICA

Many montane pteridophytes in Africa exhibit a basic distribution pattern through the east tropical African mountains with outliers to the west (Cameroon Mountain, Fernando Po) southwards to the Natal Drakensberg in South Africa, frequently also in the mountains of Madagascar, and often in the Comoro and Mascarene Islands. Such a pattern is exhibited by *Elaphoglossum hybridum* (Schelpe, 1968). A similar pattern is exhibited by the more subalpine *Xiphopteris flabelliformis* (Schelpe, 1968) of which only depauperate plants occur at the southernmost extremity of its range in the high Drakensberg. The large forest fern *Didymochlaena truncatula* has interesting outliers in northern Angola and Zaire.

Among the species from drier habitats, many ferns such as *Pellaea pectiniformis* (syn. *P. goudotii)* (Schelpe, 1968) have a predominantly south east African distribution with outliers in the Huilla Plateau of Angola or in the mountains of South West Africa/Namibia. Comparable outliers are exhibited by the marsh fern, *Thelypteris confluens* (Schelpe, 1968). Discontinuities among the African ferns vary considerably in distance and in direction. An intriguing pattern of discontinuities is that shown by *Adiantum reniforme* with isolated populations in the Canary Islands, northern Kenya and Malawi and with a subspecies in Madagascar.

Although long-distance wind dispersal in many directions cannot be discounted, it appears that many of the disjunctions are more likely to have resulted from climatic change.

ENDEMIC SPECIES

Christensen (1932), in the absence of a then up to date enumeration of African Pteridophyta, considered that two thirds were 'known in this part of the world only' and that 'with some few exceptions these endemic species are closely related either to American or Asiatic ones or belong to groups richly represented throughout the Tropics'. Despite the publication of a number of regional monographs on the African pteridophytes, only a few families have been revised on a continental scale for Africa south of the Sahara (Holttum, 1974; Launert, 1968; Schelpe, 1969). An up to date checklist is still not available.

In the same publication, Christensen (*l.c.*) estimated that about 46% of the pteridophytes of Madagascar are endemic. Regional endemicity in continental Africa is much lower. For example, in the Flora Zambesiaca area (Schelpe, 1970) only 3,7% of the pteridophyte species are endemic. In the Flora of Southern African area the percentage endemicity of the pteridophyte flora is about 19%. However, it is interesting to note that many of the distinct Southern African endemic species occur not only in the semi-arid areas (Schelpe, 1956) but also in fynbos, woodland and coastal forest. Also noteworthy, is that the nearest relatives of the localized southern Karoo endemic species, *Pellaea rufa* occur along the western sides of North and South America (Tryon, 1957).

DISCUSSION

It is accepted that long distance wind dispersal of pteridophyte spores can occur. No other reasonable explanation can be postulated for the occurrence (Tryon, 1970) of the South American fern *Eriosorus cheilanthoides* on Tristan da Cunha and Gough Islands in the South Atlantic Ocean, some 3 200 km from its nearest known American locality. Concurrently, one must ask why no other fern species from that locality in South America reached these oceanic islands and became established there.

More recently, it has become apparent that a *random* sample of six species of southern South African ferns has become established on Amsterdam Island (S. Indian Ocean, 38°S latitude) which is less than a million years old. In contrast, only two species of ferns known from southern South Africa have become established on the geologically much older Indian Ocean island of Kerguelen (47°S latitude). *Lycopodium cernuum,* widespread in South Africa, occurs around hot springs (46°C) on St Paul Island (39°S latitude) in the Indian Ocean.

Although these examples indicate the likelihood of random long-distance wind dispersal of spores at the northern limit of prevailing westerly winds, it raises the whole complex issue of the establishment of a foreign pteridophyte on new soil. Not only must the spore be transported over long distances, it must land on a substrate suitable for the germination into a gametophyte, and after fertilization to form a sporophyte. To perpetuate in its new location, conditions have to be suitable for both the gametophytic and sporophytic phases of the life history, even if apogamy is involved. However, should climatic conditions change adversely for the gametophytic stage, the sporophytic stage may well continue to exist and even multiply vegetatively. It is thought that this may well apply to populations of *Ophioglossum polyphyllum* in the Namib Desert.

A comparable case is the behaviour of fern sporophytes introduced and cultivated outdoors in a different climatic regime. For example, in the National Botanic Gardens at Kirstenbosch, which experience a winter rainfall regime, there are vigorous sporophytic plants of South African summer rainfall area ferns which never, or very rarely, produce young sporophytes. In fact, the absence of young sporophytes in a fern population would indicate that a species in a particular locality is veering towards extinction in that locality. However, a difficulty arises since few collectors attempt to gather a range of juvenile sporophytes.

The spread of ferns introduced by human activities to new continents can provide a measure of what could result from a chance long distance dispersal to a far off congenial habitat. An historical study of records of the conspicuous 'silver backed' South American fern *Pityrogramma calomelanos* (Schelpe, 1975) showed how rapidly a fern species could spread from foci of introduction and even become weeds.

The evidence available at present concerning the phytogeography of the pteridophytes in general, and the African representatives in particular, is meagre and often confusing, but indicates probabilities and possibilities. Pteridophyte taxonomists are a rare breed and relatively few of them have the opportunity or show an inclination to devote their research potential to revision, let alone monographs, of major groups on world wide or even continental scale. Progress in alpha-taxonomic evaluations on a broad scale and the plotting of distribution maps based on the data emerging from such studies form a prerequisite for future phytogeographical interpretation.

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Geographical distribution of present day Poaceae as evidence for the origin of African floras

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ABSTRACT

The major tribes and sub-families of grasses occupy worldwide latitudinal belts, which can be related to an evolutionary sequence of climatic adaptations. However, genera tend to be confined to individual continents, suggesting that grasses do not easily cross the oceans, and that the worldwide distribution of the family may have been achieved when the continents were closer together. Species distributions are likewise strongly influenced by the effect of climatic adaptation and continental isolation, but they show a number of aberrations. These are probably a legacy of climatic disturbance during the Pleistocene.

RÉSUMÉ

LA RÉPARTITION GÉOGRAPHIQUE DES POACÉES ACTUELLES EN TANT QU'ARGUMENT A L'APPUI DE L'ORIGINE DES FLORES AFRICAINES

Les principales tribus et sous-familles des graminées occupent à une échelle mondiale des zonations latitudinales qui peuvent être apparentées à une séquence évolutionnaire d'adaptations climatiques. Cependant, les genres ont tendance à être confinés à des continents isolés, ce qui laisse supposer que les graminées ne traversent pas facilement les océans et que la répartition générale de la famille dans le monde peut s'être accomplie quand les continents étaient plus rapprochés les uns des autres. Les répartitions d'espèces sont de la même façon fortement influencées par l'effet de l'adaptation climatique et de l'isolement continental, mais elles montrent un certain nombre d'aberrations. Celles-ci sont probablement un héritage de la perturbation climatique pendant le Pléistocène.

Direct evidence of past floras can only be obtained from the geological record, but it is often so scanty as to be of little help. However, present day floras are the children of the past, and contain at least some clues to their ancestry. These clues are of two kinds.

The first relates to present day distributions. Distribution maps for individual species are often instructive, but one should be wary of reading too much significance into them. This is partly because of the probabilistic element in plant dispersal. A single anomalously distributed species points only to an event so unlikely that we may never discover what it was. Ten or twenty similar distributions raise our expectations of more prosaic causal factors, and offer some hope of deducing what they might have been. The other reason for interpreting individual distributions with caution is that, by ignoring the less distinctive patterns enjoyed by the majority of species, they leave too much unsaid. I have therefore approached the problem of plant distribution by seeking first of all to understand the commonplace, using large statistically robust samples.

The second kind of clue comes from phylogeny. At its simplest, this amounts to an initial presumption that tribes evolved before genera and genera before species, offering the possibility that successive levels of the taxonomic hierarchy will afford us a sequence of glimpses into the past. Inevitably these glimpses will be grossly distorted by subsequent history, but it is nevertheless possible to glean something from them.

Of course, neither of these clues can be pursued with any confidence if they are obscured by taxonomic uncertainty. It is fortunate that, largely because of their economic importance, our taxonomic understanding of the grasses has developed to a point at which we can apply these methods with a reasonable hope that taxonomic doubt will not be a limiting factor. Let us then look at the distribution of the grasses to see what can be deduced from it.

The family

The factors contributing to the world-wide success of the grasses are fairly well-known, but it is much more difficult to assess their relative importance. A glance at the map in Cross (1980) shows that species counts are low in deserts, and it is a matter of common observation that they are also low in the shade of forests. Grasses do best in the region of seasonal rainfall between forest and desert, and it seems that their emergence as a dominant vegetation type was primarily a matter of climatic adaptation to this zone on the forest fringe. These adaptations can be seen in their life-form with its basal tillering, incorporation of the leaf-sheath into the mechanical system thus permitting the development of intercalary meristems, and the further modification of leaf-sheaths to replace the floral envelope. Undoubtedly this was associated with more subtle physiological adaptations, implied by such features as the narrow erect leaf-blades and peculiar stomata.

The second major factor was that of fire, which seems, in the African savanna at least, to have been a regular feature of the natural environment (Komarek, 1972). Grasses burn readily in the dry season, but are themselves tolerant of fires severe enough to eliminate many other life-forms, and so we have an ecosystem in which the grasses provide the fuel which ensures their own survival.

Thirdly, we have the emergence of grass-eating herbivores, and a further development of the

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ecosystem into one in which the grasses attract and sustain a degree of predation sufficient to cripple their competitors.

The final factor is man, who has joined the ecosystem and exploited it for the subsistence of himself and his livestock. In so doing, he has vastly extended its range by felling the trees which previously excluded it. Indeed, he has so confused matters that we can now only guess at what the natural grassland climate really was.

There is much that is obscure in the early history of the grasses, but the first critical step seems to have been the emergence of a life-form which was outstandingly adaptable to the environment of the forest fringe, and to subsequent events in the ecosystem that developed there. It conferred a competitive advantage sufficient for the family to occupy and to maintain its hold upon open habitats throughout the world.

Sub-families and tribes

The distribution of the major infra-familial taxa have been mapped by Hartley (1958a, 1958b, 1973), Hartley & Slater (1960) and Cross (1980), whose findings may be summarized as follows:

> Andropogoneae, Paniceae, Chloridoideae, Bambusoideae — tropical. Arundinoideae — subtropical and warm temperate zones of southern hemisphere. Pooideae — north temperate.

To understand this distribution it is necessary to take a quick look at the taxonomy of the family (Clayton, 1981). The most primitive grasses, as judged by their inflorescence structure, are the Bambusoideae, whose nearest neighbours among the Angiosperms seem to be Flagellariaceae. Since both are rain-forest groups, it is reasonable to infer that grasses arose in or near the forest. This would seem to be contradicted by their anemophilous pollination, but actually the Bambusoideae, as defined by certain anatomical peculiarities, contain three groups which can be interpreted as follows:

Bamboos. Grasses which became secondarily woody, and entered the forest to compete with trees.

Bamboo allies. A collection of broad-leaved shade-loving curios, which seem to represent the end products of unsuccessful lines that have taken refuge in the forest. Their bizarre variations give some inkling of the diversity which may once have existed before the family acquired its characteristic life-form.

Oryzeae. Although now specializing in aquatic habitats, they give some hint of the kind of open environment adjacent to forest in which the grasses might have arisen.

The next step was the Arundinoideae; true grasses of the open savanna, which are primitive in the sense that their anatomy represents the lowest common denominator of subsequent sub-families.

There then arose two divergent lines; the Chloridoideae which are evidently derived from Arundinoideae, and the Panicoideae, the derivation of which is less obvious and still somewhat controversial. They herald a new development — the evolution of Kranz anatomy and C4 metabolism. This makes photosynthesis more efficient in high temperatures and high light intensities, so it is no surprise to find that these are now the principal tropical sub-families. Nor that the Arundinoideae have been unable to compete with them, and have found a refuge in the southern subtropics.

The final step was a comparatively slight anatomical deviation from Arundinoideae. But it was evidently accompanied by a more profound physiological adaptation to cold climates, enabling the Pooideae to become the predominant sub-family of the north temperate zone.

We find, therefore, a history of physiological adaptations, whose net result has been to align the sub-families along world-wide climatic latitudinal belts. They pay little heed to ocean barriers, and even at subtribal level one is hard pressed to distinguish between continental floras.

Genera

Patterns of generic distribution may be found by dividing the world into a number of geographical units, recording each genus as present or absent in each unit, and sorting the resulting data matrix by cluster analysis. Each cluster is then displayed by transferring the presence counts of its constituent genera onto a map, and drawing in contours. The results can be summarized as follows (Clayton, 1975):

87	widespread genera
450	genera divided into seven major clusters, each of continental size
98	genera shared between geographically adjacent clusters. They link the clusters into two chains, underlining the difference already observed between tropical sub-families and the temperate Pooideae.

Evidently genera are not good travellers, two thirds of them being confined to single continents; yet we have already seen that the tribes are rather uniformly dispersed. To resolve the apparent paradox, we must look into the matter of dating.

The first positive record of grasses comes from pollen in the Palaeocene. It is followed, in the Oligocene, by fossil spikelets of *Stipa,* and by the first appearance of high-crowned teeth among fossil mammals. The high-crowned tooth strongly indicates a shift from browsing to grazing since it is an adaptation to abrasive food, such as grass whose leaf epidermis contains grains of silica. We thus have evidence that by the Oligocene grassland was an established vegetation type, containing at least one extant genus (Clayton, 1981).

Now the continents parted company in the latter part of the Cretaceous, but had not drifted very far apart by the beginning of the Tertiary. For example, Africa and America were probably some 800 km apart in the Palaeocene, moving gradually towards their present separation of 2 500 km (Raven, 1979; Raven & Axelrod, 1974). We therefore have no need to embark upon an inconclusive discussion of the feasibility of transoceanic dispersal, for the grasses evolved at a time when sea gaps were much less formidable obstacles, and I believe it was then that the tribes attained their world-wide distribution. Thereafter, genera continued to evolve, but intercontinental exchange became increasingly difficult as the gaps widened, and so generic distributions gradually assumed their present aspect of continental isolation.

Another point to emerge is that, at least by the measure of generic diversity, Africa contains the greatest of all the grassland ecosystems.

Species

Species can be analysed in much the same way as genera by scoring them as present or absent in quadrats of country size, and then applying cluster analysis. It is sometimes supposed that each species would have its own environmental optimum, resulting in a mosaic-like distribution pattern. This may be true on a local scale, but on a wider scale species are found to be rather strongly clustered, an effect which probably stems from entrainment with the dominant, climatically determined life-form. Individual members of a cluster may vary considerably in their environmental amplitude, so that the cluster has no sharp boundaries, but fades away gradually at the edges, and is best mapped by a form of contouring. This effect may well be exaggerated in the case of grasses, which display a great capacity for infiltrating the seral stages of communities from which they would otherwise be excluded. Certainly the grass flora of a given area is usually composed of species from several overlapping clusters or phytochoria.

When mapped out, smaller clusters tend to be nested within larger ones, a phenomenon which affords a natural basis for their classification; they have been described and mapped by Clayton & Cope (1980). The largest clusters of all are termed Kingdoms, of which there are probably five (the doubts concern South America, whose taxonomy is still very confused). Evidently this category reflects the continental isolation that we have already seen among genera.

The African grass flora is almost entirely Palaeo-tropical, but there are a few exceptions. Thus the Pan-temperate Kingdom extends to North Africa, and is represented south of the Sahara by a number of weedy introductions. There are also about 40 pan-tropical weeds of uncertain domicile, and a trace of Neo-tropical species; most of the latter are clearly introduced weeds, leaving about a dozen whose status is still arguable.

The Palaeo-tropical Kingdom may be divided into two Subkingdoms, evidently representing a lesser degree of continental isolation. The Deccan-Malaysian Subkingdom need not greatly concern us, apart from noting a sprinkling of records along the East African coast which are almost certainly the consequence of coastwise trading; the few records in West Africa are even more obviously associated with the hinterland of ports. The other half of the Palaeo-tropical Kingdom is the Afro-Arabian Subkingdom. This is the only purely notional unit which it has been found necessary to introduce, there being no grasses whose distribution matches its limits. However, its recognition serves to emphasize that African grass species are essentially African in origin.

The Afro-Arabian Subkingdom contains six Regions. With the possible exception of Madagascar, these Regions coincide with major climatically determined vegetation belts. They are in equilibrium with the environment, and their members have occupied all the territory available to them. Whatever migratory episodes they have suffered in the past, the regional species are those which have successfully adjusted their distribution to conform with current climatic patterns.

Domains within Regions are rather more interesting. Thus we find that within the Guineo-Congolan Region there are separate Guinean and Congolan Domains. There seems to be no obvious climatic reason why they should be thus confined, and the existence of separate species pools is probably attributable to difficulty in dispersing across the uplands of the Cameroon mountain range.

The Sudano-Zambezian Region contains Sudanian and Afro-oriental Subregions, corresponding to environmental differences sometimes informally summarized by the terms Lowland and Upland Africa. It is not so much a matter of absolute climatic differences or a major barrier at the junction of the Subregions, but rather that suitable habitats are sparser on the opposite side, making migration more difficult. The Subregional species are those which have not yet achieved it.

The Afro-oriental Subregion contains three Domains — Ethiopian, Zambezian and Transvaal. It may be that local climatic differences could account for the existence of three separate species pools within the savanna, but there is another possibility. The Saharo-Sindian Region dips southward to Tanzania and then reappears as an outlier in South West Africa, implying the former existence of an arid corridor between these now disjunct areas. The corridor would have surrounded the Ethiopian Domain and driven between the Zambezian and Transvaal Domains, permitting their floras to evolve in isolation. Although the Domains are now connected by continuous savanna, a unified species pool has not yet been fully restored.

Endemics

I have presented a model which relates African species pools to the major climatic zones through entrainment with the dominant vegetation type. They are sometimes subdivided when free dispersal is hindered by the filter effect of physical obstacles. They are occasionally distorted by an unresolved legacy of past climatic change. I have so far said little about the other main driving force of chorology, which is speciation.

This is a subject on which it is easy to theorize, but difficult to acquire factual evidence. One of the traditional approaches to the problem is through endemism, and attempts to distinguish between centres of origin and refugia. The frequency of one-country endemics has been mapped by Clayton & Cope (1980), revealing classical centres in Fouta-Djallon and Ethiopia, but elsewhere the pattern is very confused. The highest counts occur in South Africa, Madagascar, Peninsular India, South East Asia and Australia, where isolation is clearly an important factor. Otherwise they are strongly correlated with mountain topography (the pediplain of the Congo-Zambezi watershed is an unexplained exception), and form long chains rather than discrete centres. In short, the concept of endemic centres, at least in its simple form, is shown to be somewhat naive and not particularly helpful. The geography of speciation remains an open question, but I would suggest that the striking difference between the mountains and the plains lies not so much with active speciation in the former, as with ruthless extinction in the latter.

The Afro-montane Region

There remains the matter of the Afro-montane flora, which presents a number of unusual and fascinating problems. Its grasses may be defined as those whose distribution lies mainly above 2 000 m, or as those which belong to the sub-family Pooideae; both definitions give substantially the same species list. They can be divided into four elements (Clayton, 1976):

1. A small element from the Pan-temperate Kingdom and its subdivisions. Most are widespread weedy species almost certainly introduced with agriculture. A very few are more characteristic of moorland than ruderal habitats, hinting at the possibility of a direct migratory route (birds?) between the moorlands of Europe and Africa.
2. The 'Afro-montane' species with a lower altitudinal limit of around 2 000 m, which show a quite surprising degree of uniformity on widely separated mountains. They have attracted much debate, the consensus of opinion being that dispersal was facilitated by 'stepping stones', during a period of cooler climates when suitable habitats developed on a number of lower peaks.
3. The 'Afro-alpine' species with a lower altitude limit of around 3 000 m, which show a quite different pattern of distribution, being either endemic to a single mountain, or sharing apparently random pairs of adjacent mountains. It seems that this element is the result of speciation to occupy the empty alpine environment created by the uplift of the great volcanoes and the Ruwenzori fault block; and that there has been no assured migratory route between peaks, but some random dispersal dependent on chance events.
4. A small South African element, being a northward extension of another montane flora of pooid grasses centred on the Drakensberg range.

We have already seen that the Pooideae probably arose in Eurasia, and it is tempting to relate their arrival in Africa to the Plio-Pleistocene creation of the great volcanoes on which they are now so prominent. But the concept of opportunistic migration from Europe does not altogether account for the presence of a second pooid flora in South Africa. It is difficult to estimate altitudes in Miocene Africa due to the extensive upwarping that occurred towards the end of this period, but there is evidence that a number of the older mountain blocks which we see today (particularly the Ethiopian massif) then stood at about 2 000 m. I believe that the pooid immigration was to these mountains, sufficiently long ago for two separate indigenous floras to differentiate. They are essentially native floras of long standing, and it would be misleading to think of them as Pan-temperate outliers.

The montane flora is obviously a distinct ecological entity, but its treatment as a separate Afro-montane chorological Region raises philosophical problems. It would seem to imply that the floras of adjacent ecological habitats could be independently distributed. There is no evidence that this is true of, say, swamps and dry land in Africa. Nor does it seem applicable to the montane flora of tropical Asia, where mountains occur as ranges rather than inselbergs. Is it, in fact, true of African mountains? If isochores are plotted for the Afro-montane grasses, they are found to be very similar to those of the Ethiopian Domain, implying that adjacent lowland and montane floras have not achieved any significant degree of independent migration.

Of course, at generic level, the lowland and montane floras are very different. Should we take account of generic chorology, with its very different time scale, when defining floristic elements, and if so where will this lead us? The montane grasses of the Old World tropics are certainly a special case, but treating them as Regional phytochoria seems to raise more problems than it solves.

I have presented a picture of how the grasses achieved their present distribution in Africa. It is essentially a fairly simple picture, for the use of large samples has averaged out idiosyncracies of ecological preferences, habitat distribution, community competition and dispersal probability. I am very conscious that gaps in the factual evidence have been bridged by speculation, and that the results pertain to only a single family. I look forward to seeing their generality tested by similar analyses of other families.

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Geographical distribution of present-day Cape taxa and their phytogeographical significance

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ABSTRACT

The Cape Flora, one of the six floral kingdoms recognized by phytogeographers, is remarkable for its species richness and high degree of endemism, but no overall statistics are as yet available. Several long-term projects have recently been started to enumerate all the species and to record their distribution patterns. The latter aspect has been completed for 1 936 species from the three most characteristic families, i.e. Restionaceae, Ericaceae and Proteaceae, the endemic families and some of the largest genera, i. e. *Aspalathus* and *Muraltia*. Computer analysis of the distribution patterns is being undertaken and the species concentrations and centres of endemism are being calculated. The concentration of species in the mountains of the south-western Cape is confirmed and the grid square 3418 BB is found to be the richest. For the groups dealt with, the degree of endemism was found to be as high as 98%. The phytogeographical centres so far outlined agree with those of Weimarck.

RÉSUMÉ

RÉPARTITION GÉOGRAPHIQUE DE TAXONS ACTUELS DU CAP ET LEUR SIGNIFICATION PHYTOGÉOGRAPHIQUE

La flore du Cap, un des six empires floristiques reconnus par les phytogéographes, est remarquable pour sa richesse en espèces et son haut degré d'endémisme, mais aucune statistique d'ensemble n'est encore disponible. Plusieurs projets à long terme ont été rédemment entrepris en vu d'énumérer toutes les espèces et de noter leurs modes de distribution. Ce dernier aspect a été réalisé pour 1936 espèces appartenant aux trois familles les plus caractéristiques, c'est à dire les Restionacées, les Ericacées et les Proteacées, aux familles endémiques et à certains des plus grands genres, comme Aspalathus *et* Muraltia. *Une analyse par ordinateur des modes de répartition est en cours de réalisation et les concentrations en espèces et centres d'endémisme sont actuellement calculés. La concentration en espèces dans les montagnes du sud-ouest du Cap est confirmée et le carré du quadrillage cartographique 3418 BB se révèle être le plus riche. Pour les groupès étudiés, le degré endémisme a pu s'élever jusqu'à 98%. Les centres phytogéographiqies définis jusqu'à présent s'accordent avec ceux de Weimarck.*

INTRODUCTION

The flora of the southernmost tip of Africa is one of great biogeographical interest because of its remarkable richness and high percentage of endemic species. This led Takhtajan (1969) and Good (1974) to recognize the Cape Floral Kingdom, one of the six floristic kingdoms of the world, equal to their Palaeotropical Kingdom which consists of the whole of the rest of Africa and south-east Asia.

Marloth (1908) put the number of species 'in the Cape' at about 6 000, but this figure is certainly low when one takes into account the more complete records and modern monographs of recent years. Goldblatt (1978) gives the figure of 8 550 species occurring in the Cape Region (sensu Goldblatt), a mere 89 000 km^2, and comprising 42% of the southern African flora. An analysis of the latter flora with an emphasis on the Cape Region is given by him.

Much has been written about the phytogeography and evolution of this unique Cape Flora, the most comprehensive papers being Marloth (1908), Weimarck (1941), Levyns (1964) and some excellent recent reviews by Taylor (1978, 1980), Goldblatt (1978) and Axelrod & Raven (1978). The most significant one in regard to phytogeography is that of Weimarck entitled 'Phytogeographical Groups, Centres and Intervals in the Cape Flora' in which he analysed 462 species. In much of the work repetition of previous results has of necessity been prevalent except when authors have been able to interpret the results of their own revisions.

Since 1941 much more collecting has been done and this has extended the distribution ranges of many taxa and increased the size of the flora and here we must acknowledge the outstanding work done by Miss E. Esterhuysen. Critical revisionary work has resulted in the recognition of many synonyms. This made an objective re-appraisal of Weimarck's work of recognizing phytogeographic centres within the Cape Flora a necessity.

In addition to phytogeography, there has been much discussion on the possible origins and migrations of the Cape Flora (Levyns, 1938, 1964; Adamson, 1958; Axelrod & Raven 1978). The bulk of the Flora clearly shows a northern origin, whereas some elements may be remnants of an ancient Gondwanaland flora. During the Pleistocene extensive fluctuations in the area of the Flora were thought to have occurred (Levyns, 1964; Axelrod & Raven, 1978) with the Flora being displaced from its

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present habitat by extension of the temperate forest. A thorough analysis of the phytogeographical patterns in the present Cape Flora may cast some light on its history.

Two major issues had to be resolved at the outset first, what area had to be sampled and second, what taxa are typical of the Cape Flora.

The definition of the Cape Flora and the boundaries of its area have also been discussed by many authors. The southern and south-western Cape (Fig. 1) contain three main and distinct vegetation types (Levyns 1964; Taylor 1978):

1. Sclerophyll type which forms the Cape Fynbos vegetation that is the home of the distinctive Cape Flora (Levyns, 1964; Oliver, 1977; Taylor, 1978).
2. Temperate Evergreen Forest of the Knysna area.
3. Karroid Broken Veld of the Karoo-Namib Region.

In many areas tongues of vegetation of the above types occur deep within each other thus rendering exact and simple definition of their boundaries very difficult. This led Goldblatt (1978) to choose a broad geographic unit as the Cape Floral Region for the purposes of his survey. We have sampled the entire area of the main block of fynbos as delimited by Kruger (1979) (Fig. 2), but also included outliers south of 30°S (plus a few in Namaqualand and the Richtersveld) and west of 28°E.

The taxa constituting the Cape Flora are those forming fynbos vegetation and consequently can be defined as those that are most diversified within the area of the fynbos vegetation although outliers may be found in other vegetation types as far afield as North Africa and, in some cases, on other continents. Physiognomically, fynbos is characterized by three elements, namely restioid, ericoid and proteoid. The degree to which a taxon may be considered as a 'typical Cape Floral taxon' depends on the extent to which the taxon shares both distributional and physiognomic criteria.

A long-term project has been started and aims at recording by means of maps the distribution patterns of taxa occurring within the Cape Floral Region. This paper presents the preliminary results. Another long-term project to record the exact number of species within the Cape Floral Kingdom in the form of a checklist has been under way for the last few years (Goldblatt & Fairall, pers. comm.). These two projects should complement each other very well.

METHODS

The following taxa were selected as representing typical Cape Floral Region taxa. Recently published revisions were available for *Leucadendron* (Williams, 1972), *Leucospermum* (Rourke, 1972), *Sorocephalus* and *Spatalla* (Rourke, 1969), *Diastella* (Rourke, 1976) in the Proteaceae; *Aspalathus* (Dahlgren, 1960–1968) in the Fabaceae; Penaeaceae (Dahlgren, 1967–1971); *Adenandra* (Strid, 1972) in the Rutaceae; *Bobartia* (Strid, 1974) in the Iridaceae; *Muraltia* (Levyns, 1954) in the Polygalaceae; *Anaxeton* (Lundgren, 1972) in the Asteraceae. Where revisions are in progress information was provided by the monographers, i.e. Diosmeae-Rutaceae (Williams), remainder of the Proteaceae (Rourke), minor genera of the Ericaceae (Oliver), *Psoralea* (Stirton). For the remainder of the taxa, distributional data were derived from the numerous herbarium specimens housed in the following herbaria: *Erica* (PRE, BOL, NBG, SAM, STE, GRA, NH); Restionaceae (BOL, NBG, SAM, PRE) with checking by Linder and Esterhuysen; Bruniaceae (BOL; NBG; PRE) and

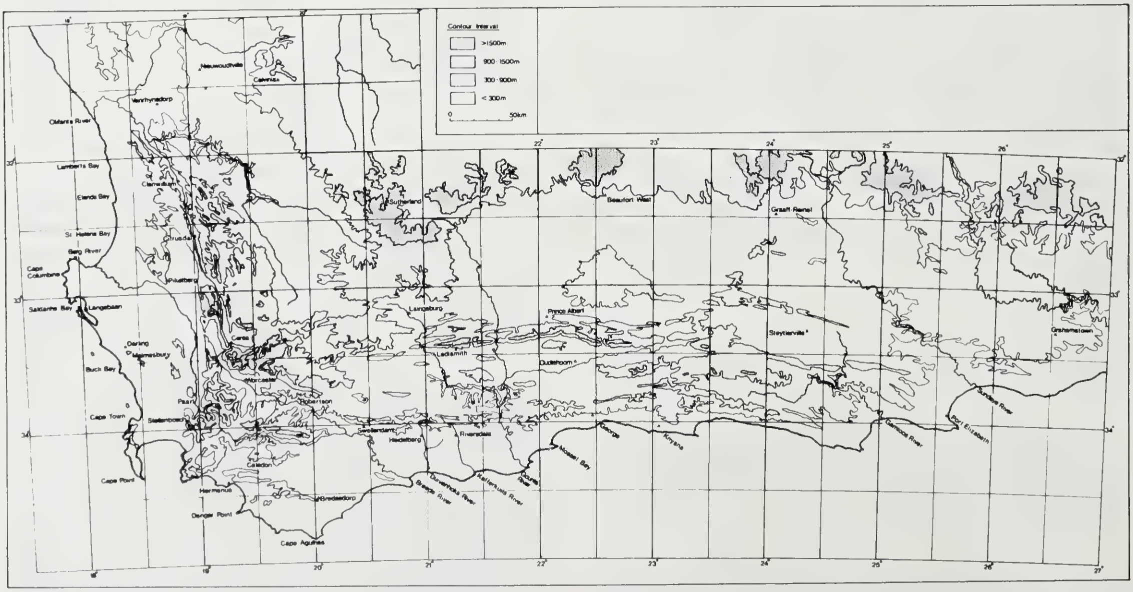

FIG. 1.—Main area covered in this survey.

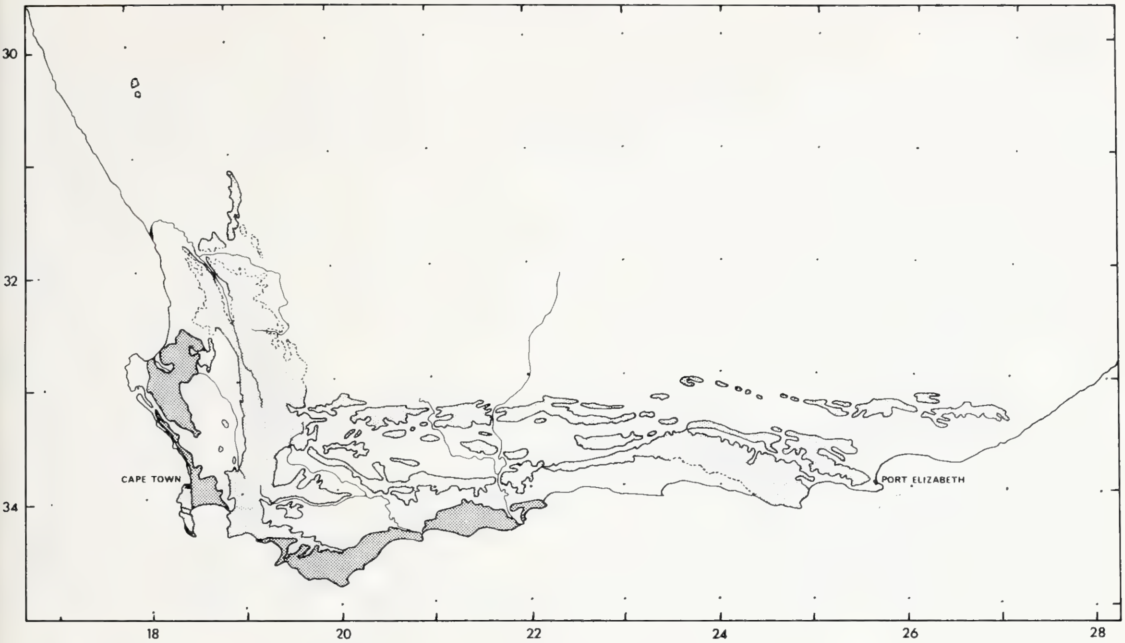

FIG. 2.—Distribution of fynbos. Heavy shading indicates coastal fynbos and light shading, mountain fynbos (after Kruger, 1979).

records additional to Levyns's revision of *Muraltia* (PRE). We had, of necessity, to accept the identifications on the specimens. In some cases these will be erroneous, but it was felt that the percentage of incorrect identifications would not affect the survey to any extent. The species were listed and numbered following the taxonomic order within each genus and family in the revisions and the herbaria. This selection of taxa gave a sample of 1 936 species with 1 810 occurring within the sample area.

For each species all specimens were recorded and coded according to the grid reference system of Edwards & Leistner (1971). This gives a quarter degree square unit with an area 23 × 23 km of ± 760 km^2 in the south-western Cape. The scale of this grid system and its positioning was found very suitable for covering the south-western Cape. Grids were only recorded for precisely locatable localities. The grids in the study area were numbered in a linear sequence from west to east from Nos 1, 2 and 3 near Cape Agulhas to No. 311 in the Richtersveld. Lists were compiled of the quarter degrees and maps compiled by hand for each species. The grids and species were then encoded solely on presence per grid with no weighting for frequency per grid. Weighting is not possible from herbarium records alone and can only be done after detailed field surveys.

The data were grouped using the PHYTOTAB program package (Westfall *et al.*, 1982) on an IBM 370/148 computer. This program package provides a preliminary grouping of species as well as grid squares based on Jaccard's community coefficient (Müller-Dombois & Ellenberg, 1974). PHYTOTAB 20 provided an objective clustering program to facilitate initial grouping of the data matrix. Final grouping was obtained by user sequencing of parameters according to the techniques used for Braun-Blanquet tablework (Westhoff & Van der Maarel, 1973; Werger, 1974). This program was developed for relevé/species analyses in vegetation surveys and seemed eminently suitable for the phytogeographic analyses of this project. The maximum matrix size of the program is 2 000 relevés by 2 000 species, hence the restriction on the number of species chosen for the preliminary survey.

In a recent survey of a very similar type, Denys (1980) produced a tentative phytogeographical division of tropical Africa based on mathematical analysis of published maps. His complicated analysis of 494 taxa used factor analysis.

RESULTS AND DISCUSSION

Patterns of species richness

The first print-out using PHYTOTAB 10 provided a basic matrix for checking input data, but also provided totals of the number of species per quarter degree square and of quarter degrees per species. This appeared on all subsequent print-outs as a cross-check.

The total number of species per quarter degree square is shown in Fig. 3, but as a percentage of the total sample. Values are to the nearest whole number. Maps for each family and/or genus were produced by visual inspection of the print-out (Figs 4–12). Isoflor maps were produced for the three major families to show the nodes of species richness (Figs 3B, 4B, 5B & 7B).

Levyns (1938) was the first to show with a few small genera that the Caledon District is the centre

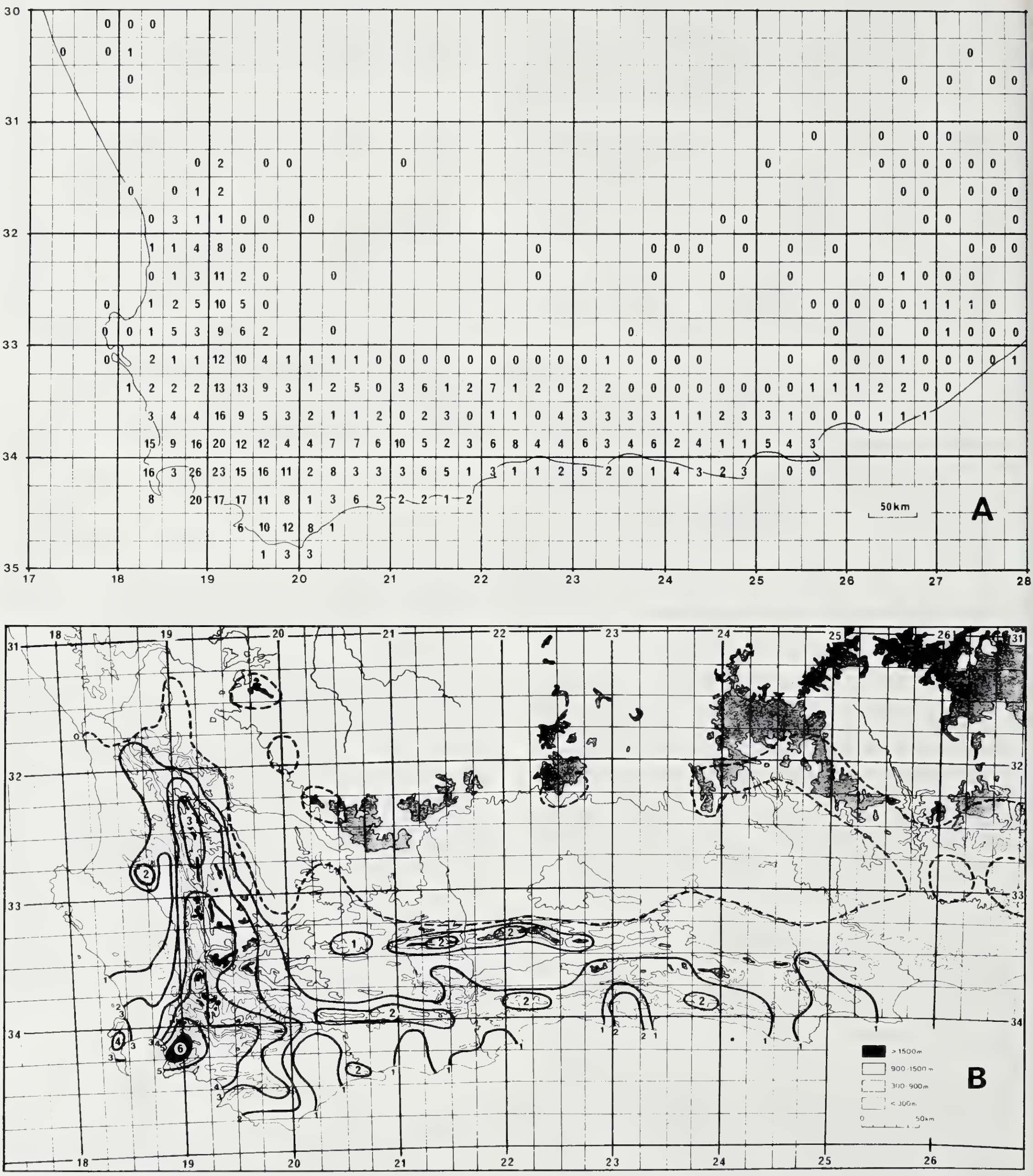

FIG. 3.—Distribution of the total number of species dealt with in this survey. A, expressed as a percentage to the nearest whole number per grid square (0 represents <1%); B, as isoflors (0–1 = 0–2%; 1–2 = 3–4%; 2–3 = 5–9%; 3–4 = 10–14%; 4–5 = 15–19%; 5–6 = 20–24%; 6 = 26%).

of species richness with a reduction in numbers to the north and east. She suggested that this pattern may be used to define true Cape genera. All our maps confirm this view. The more detailed analysis here indicates that the quarter degree, 3418 BB centred on Sir Lowry's Pass and the Hottentots-Holland Mountains is the richest area in the Cape Floral Region with 26% (476 species) of the sample. This includes 207 species of Ericaceae (with 175 species in the genus *Erica*), 74 species of Restionaceae and 70 species of Proteaceae.

This is a remarkable concentration of species and is made more so when one realizes that approximately 25% of the grid is sea and another 25% inhospitable flats. The remainder consists of mountain range rising from sea-level to 1 268 m within only three kilometres and an upland plateau at ± 450 m. In this grid square, all three geological formations of the Cape System occur, i.e. Table Mountain Sandstone, Bokkeveld Shale and Cape Granite. The average annual rainfall gradient is extreme from 700 mm on the flats to 3 600 mm at the

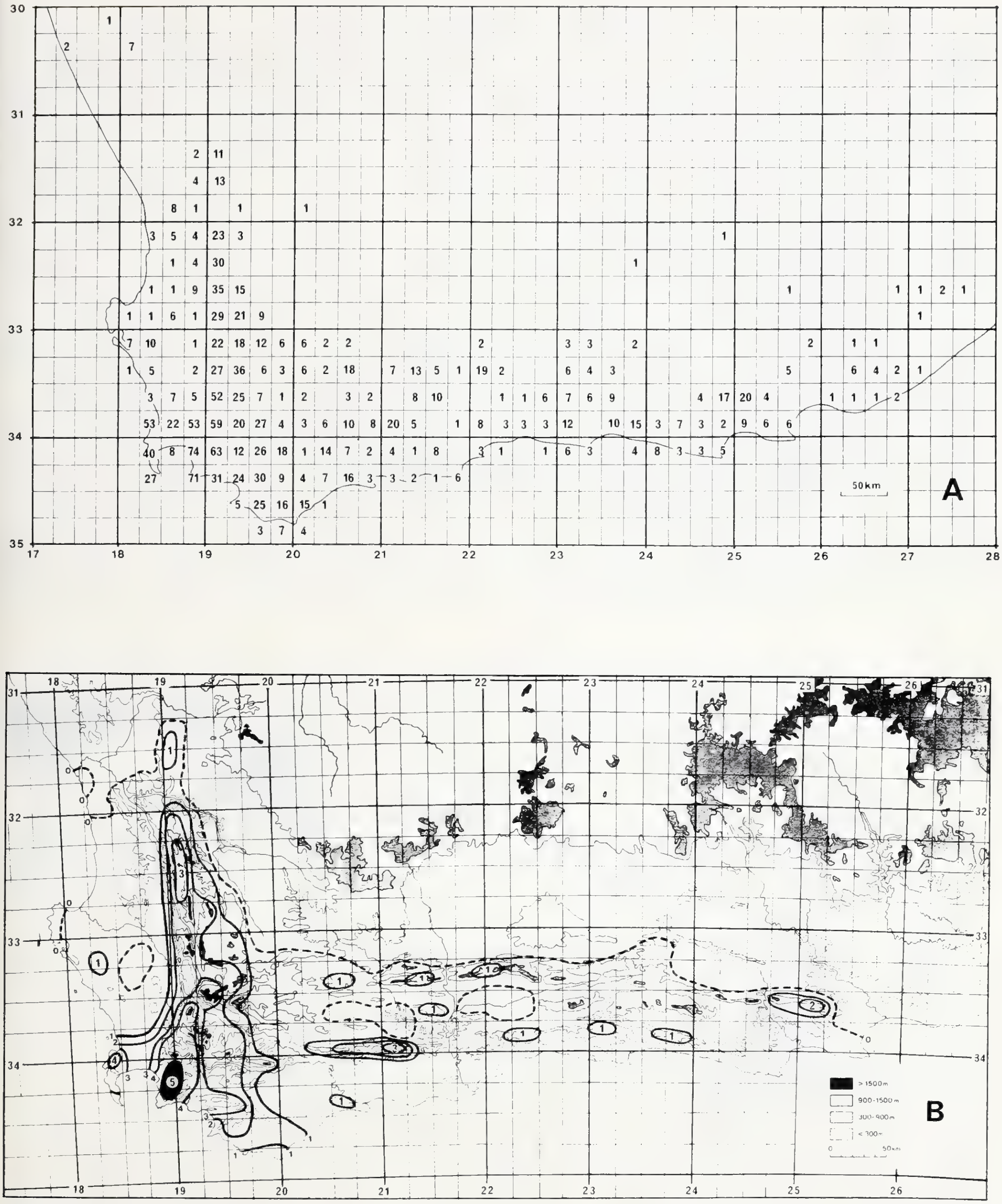

FIG. 4.—Distribution of Restionaceae. A, the number of species per grid square; B, as isoflors (0–1 = 0–9 species; 1–2 = 10–19 species; 2–3 = 20–39 species; 3–4 = 30–49 species; 4–5 = 50–69 species; 5 = 70 species→).

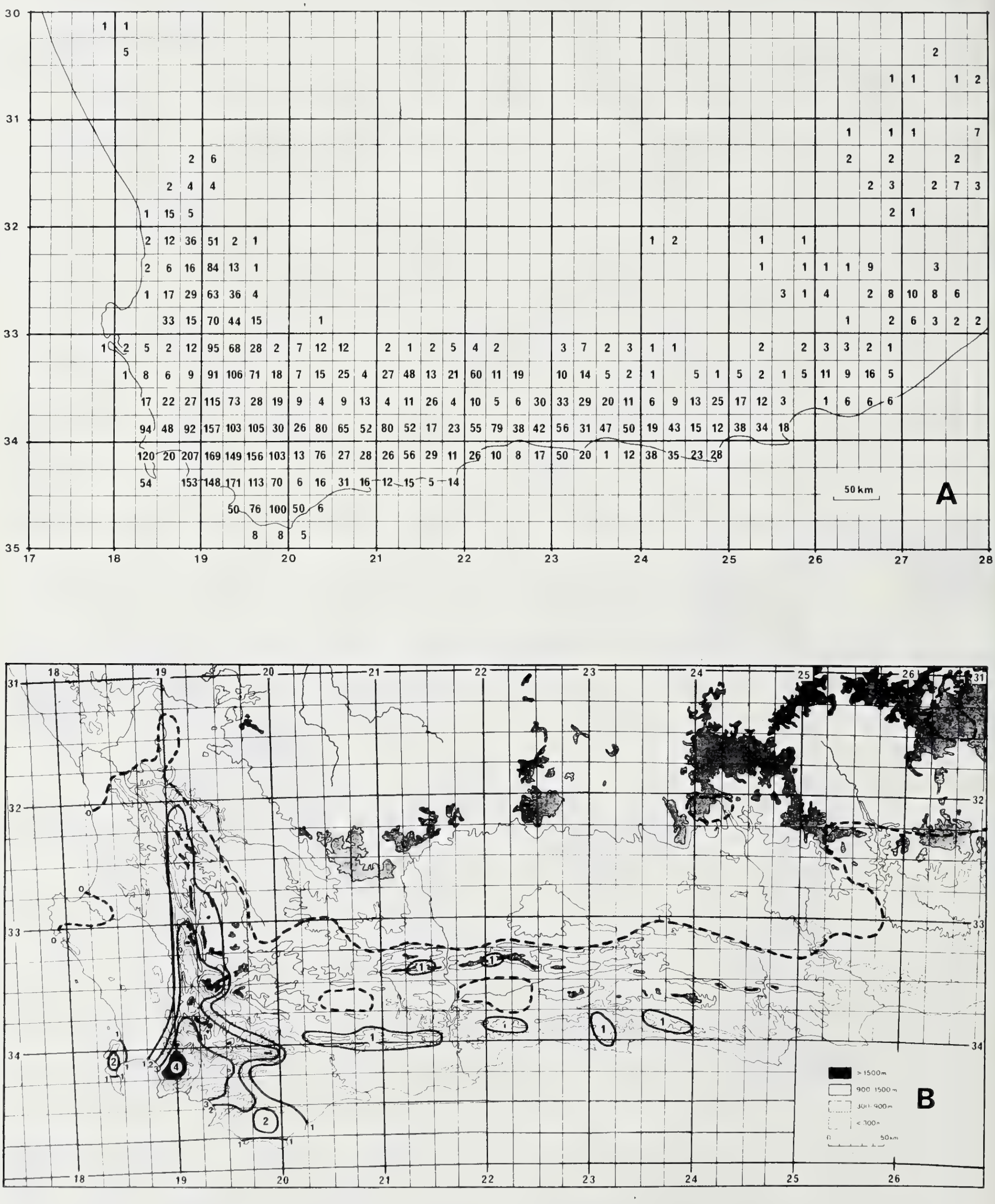

FIG. 5.—Distribution of Ericaceae. A, the number of species per grid square; B, as isoflors (0−1 = 0−49 species; 1−2 = 50−99 species; 2−3 = 100−149 species; 3−4 = 150−199 species; 4 = 200 species→).

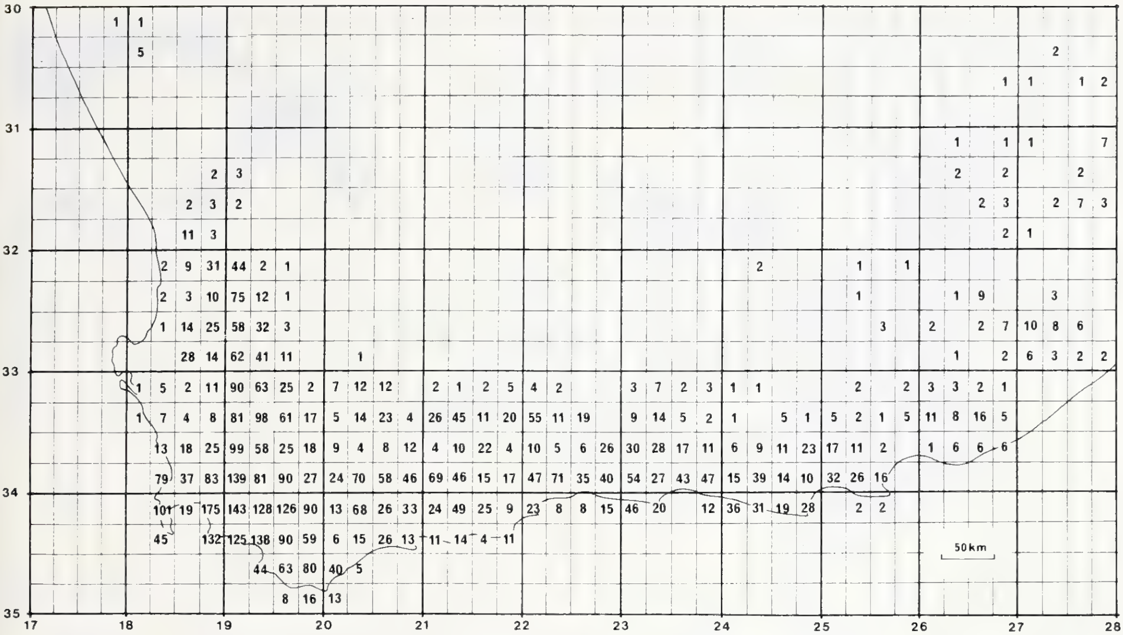

FIG. 6.—Distribution of the genus *Erica* with the number of species per grid square.

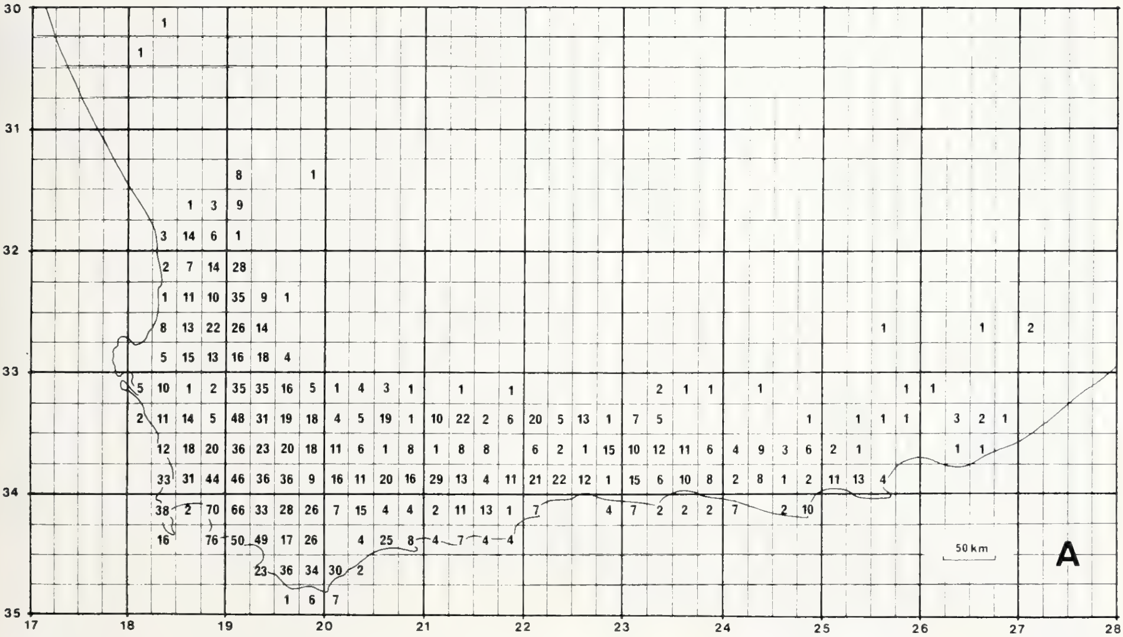

FIG. 7A.—Distribution of Proteaceae. The number of species per grid square.

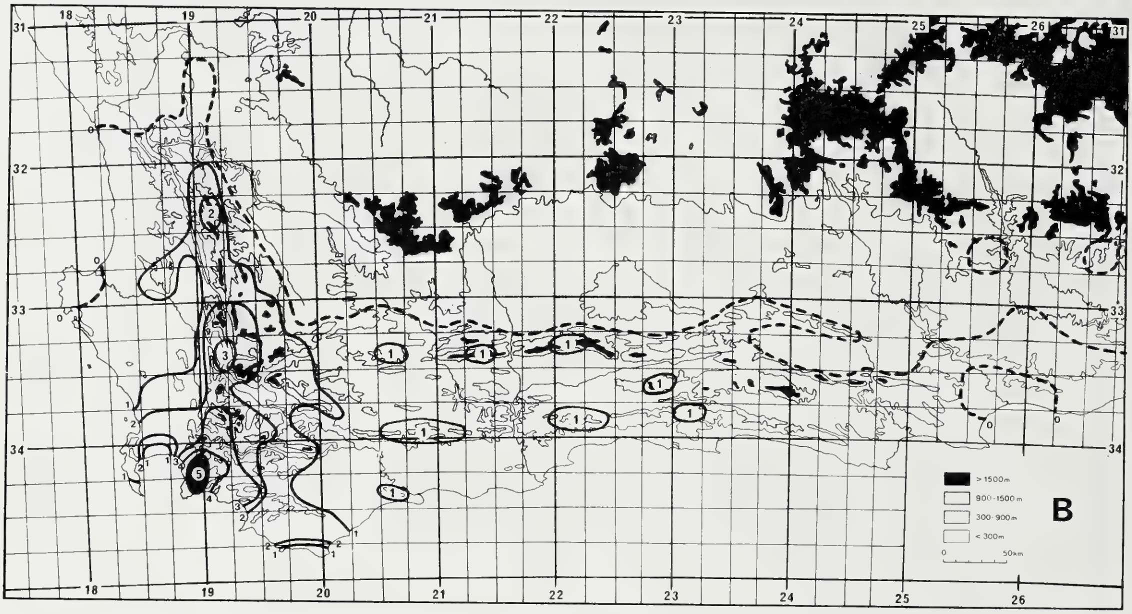

FIG. 7B.—Distribution of Proteaceae. As isoflors (0–1 = 0–14 species; 1–2 = 15–29 species; 2–3 = 30–44 species; 3–4 = 45–59 species; 4–5 = 60–69 species; 5 = 70 species→).

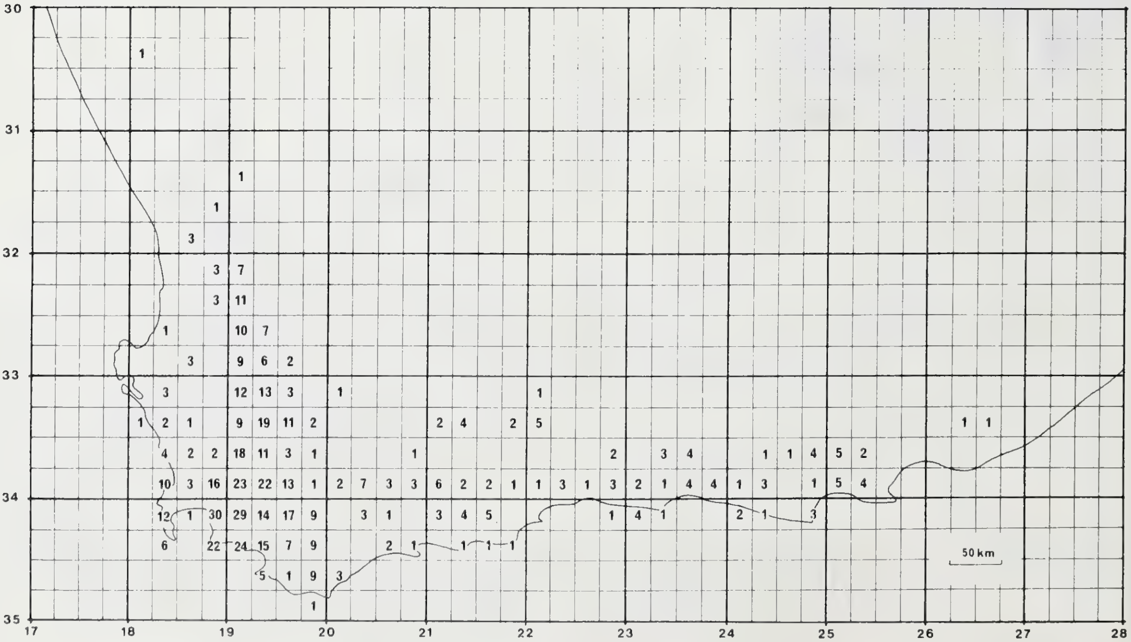

FIG. 8.—Distribution of Bruniaceae with the number of species per grid square.

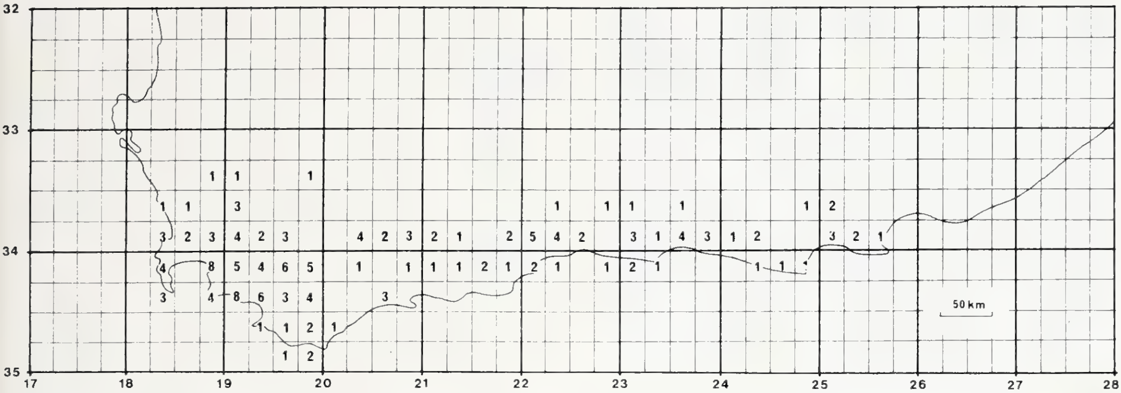

FIG. 9.—Distribution of Penaeaceae with the number of species per grid square.

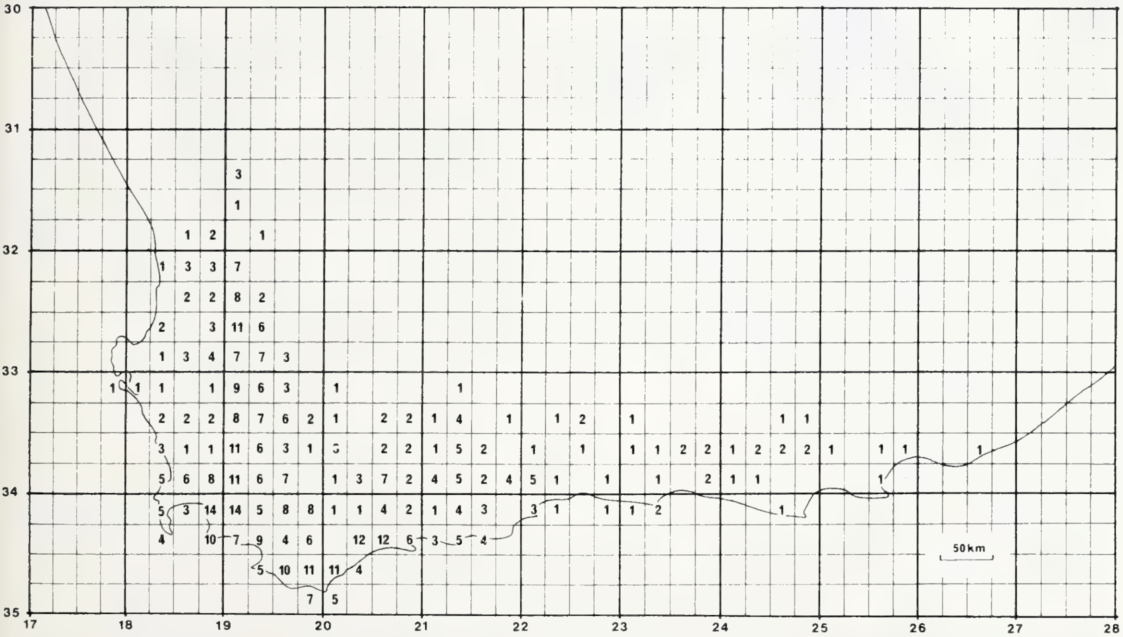

FIG. 10.—Distribution of the tribe Diosmeae (Rutaceae), excluding the genus *Agathosma*, with the number of species per grid square.

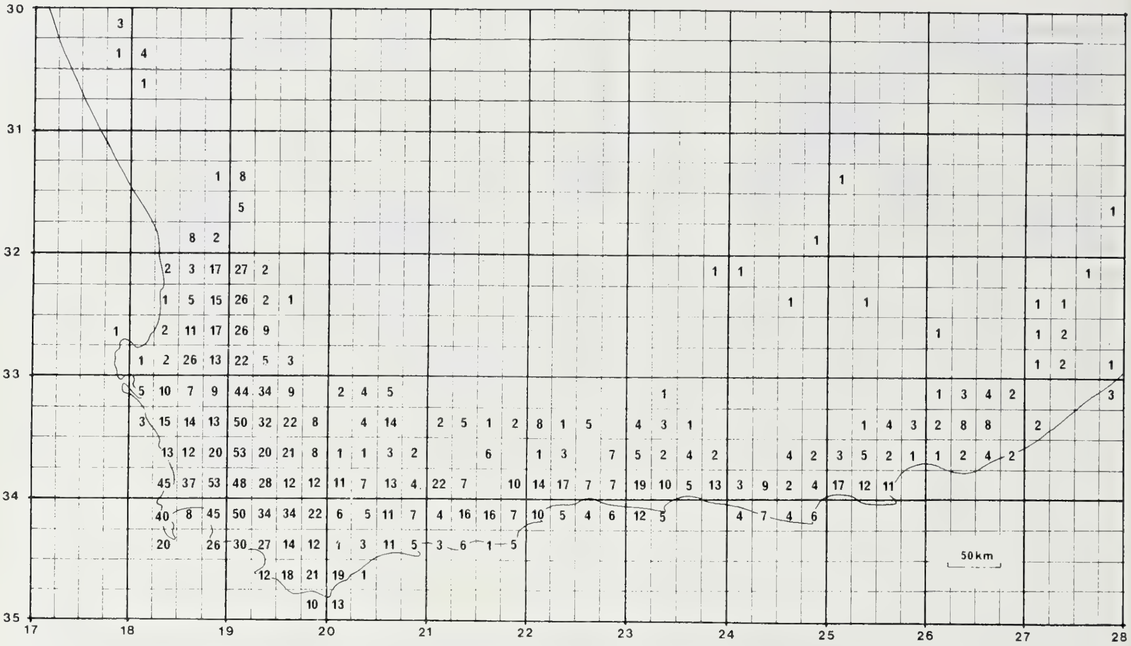

FIG. 11.—Distribution of the genus *Aspalathus* (Fabaceae) with the number of species per grid square.

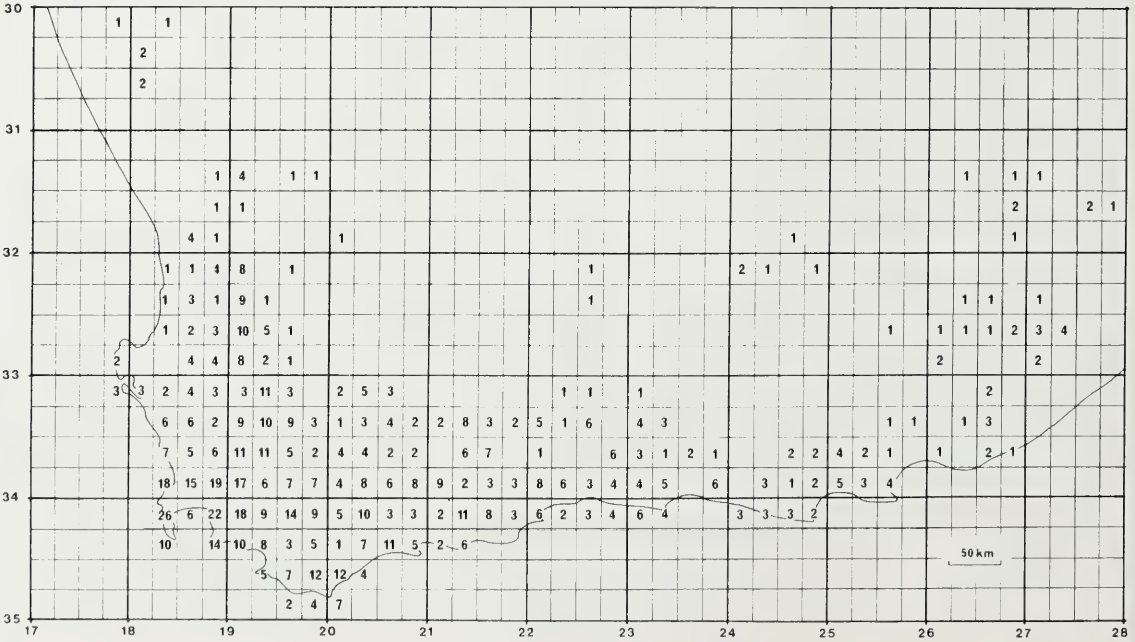

FIG. 12.—Distribution of the genus *Muraltia* (Polygalaceae) with the number of species per grid square.

highest point again within a very short distance. The precipitation pattern varies from summer drought regime to all-year rainfall on the summits caused by deposition of moisture from south-easterly clouds which is not recorded in the annual rainfall figure above (Marloth, 1904; Boucher, 1978).

The maps also indicate that there is a species richness gradient (1) from the Hottentots-Holland northwards to the Cedarberg, where there is a slight centre of richness (2) south-eastwards to the Bredasdorp/Agulhas area (3) eastwards along the main chain of mountains of the southern Cape, i.e. Langeberg/Outeniqua/Tzitzikama, to Port Elizabeth (4) an inland gradient along the Swartberg Range and (5) a centre of richness on the Cape Peninsula.

A word of caution should be expressed when looking at these results. To some extent the patterns produced are artifacts produced by uneven collecting. Herbarium records depend on the accessibility and 'popularity' of areas. Areas such as the Cape Peninsula, Sir Lowry's Pass, central Cedarberg are well collected. This is very evident in the eastern parts such as the Witteberg, Seven Weeks Poort, Swartberg Pass, Meirings Poort, Garcia's Pass and the Outeniqua/Montagu Pass. However, one could extrapolate these figures to the rest of the mountain ranges without affecting the results unduly.

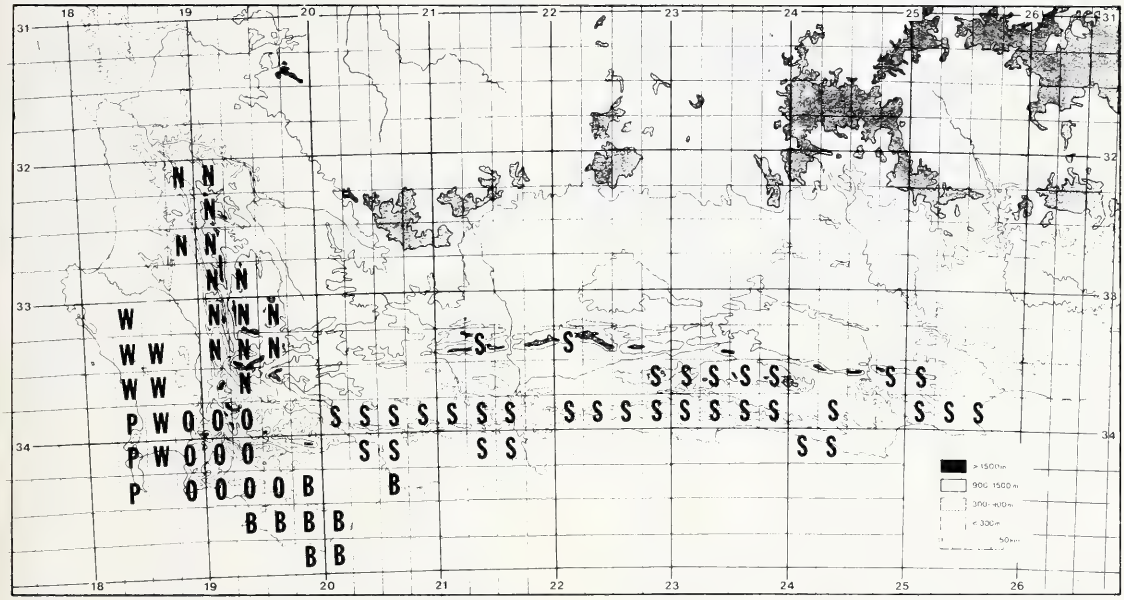

FIG. 13.—Phytogeographical centres in the Cape Flora as indicated by the present survey (N, Northern; W, West coastal; P, Peninsula; O, South-Western; B, Bredasdorp; S, Southern).

Phytogeographical centres

The next section of the program PHYTOTAB 20 grouped the grid localities wherever possible into large or small units which were then visually checked for grouping. The resulting six basic groups were plotted onto a grid map (Fig. 13). These groups covered six distinct separate areas which will be referred to as the Northern Centre, the Peninsula Centre, the South-western Centre, the West Coast Centre, the Bredasdorp Centre and the Southern Centre. Several areas of grid squares were not grouped in this program, due either to inadequate sampling and records or to their being intermediate between centres. The coastal flats of the north-west certainly group with the West Coast centre, and the southern coastal flats should be included with the Bredasdorp Centre.

The Rivier Zonder Eind mountains are probably intermediate between the South-western and Southern Centres, whereas the Robertson to Witteberg mountains are probably intermediate between the Northern, South-western and Southern Centres. Outliers in Namaqualand, the Karoo mountains and Eastern Cape mountains would be related to their nearest centres. These six centres agree with the major edaphic and climatic systems in the south-western and southern Cape outlined in Table 1.

On the whole, these centres agree with the centres defined by Weimarck (1941). (Fig. 14). His North-western Centre is clearly the same as ours.

We have a grouping equivalent to his South-western Centre which is bounded by the Berg River in the north and the Breede River in the east, but with a slight discrepancy in the Tulbagh area. However, very distinct groupings occurred within our centre that turn out to be equivalent to Weimarck's subcentres, i.e. Cape Peninsula, West Coast Flats, Central South-western Mountains and Bredasdorp.

The main discrepancy lies with the centres to the east where we are unable, in the preliminary sort, to obtain any really significant groupings. There were slight indications of groupings in the Langeberg, the Tzitzikama/Kouga area and the far south-east.

TABLE 1.—Phytogeographical centres indicated in this survey with the main edaphic and climatic conditions prevailing in each one (TMS = Table Mountain Sandstone)

Centre	Substrate	Climate	Rainfall (mm p.a.)
Northern	TMS mountains	Summer drought	300–1600 North 3000 South
West Coast	Recent TMS sand	Summer drought	200–500
Peninsula	TMS mountains	Winter rains Summer clouds	600–2400
South-Western	TMS mountains	Winter rains Summer clouds	700–3600
Bredasdorp	Recent calcrete and sand	Summer drought	300–700
Southern	TMS mountains	All year rain	300–1400

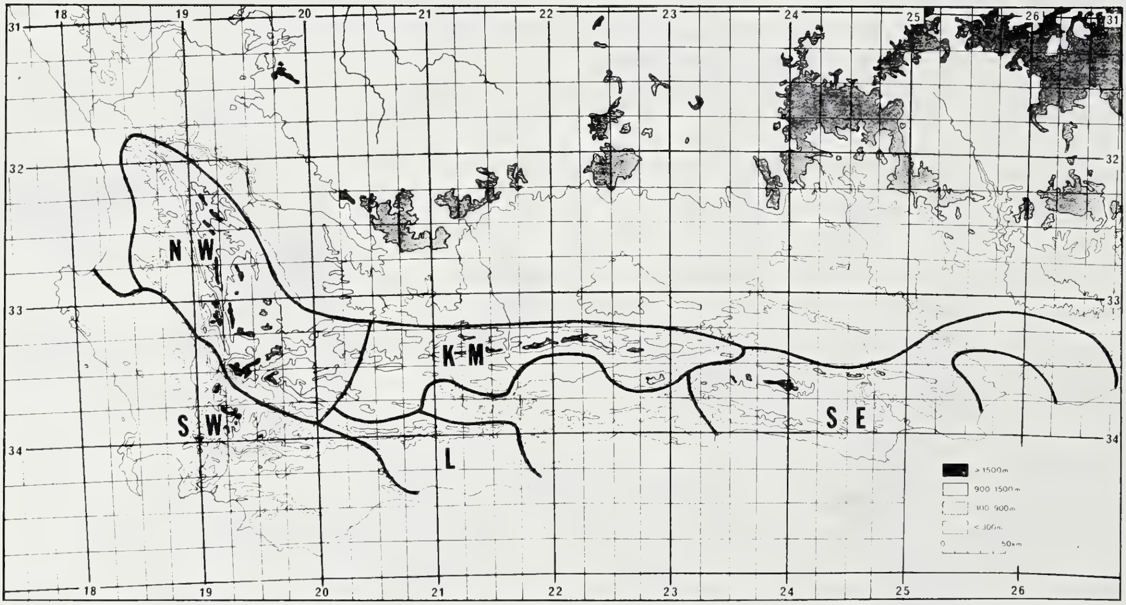

FIG. 14.—Phytogeographical centres in the Cape Flora according to Weimarck, 1941 (NW, North-western; SW, South-western; L, Langeberg; KM, Karoo Mountain).

Endemism

The Cape Flora is renowned both for the high degree of endemism to the Cape Floral Region and for a high degree of endemism locally. From a literature survey, Weimarck (1941) showed that of the 3 692 species represented within the Cape Flora 3 536, i.e. 95,8%, are endemic. Table 2 gives a summary of the endemism in the families and genera included in the present survey. With some 2 183 species endemic in the Cape Region out of an estimated total of 2 235 species represented in Africa a figure of 98% is obtained. This extremely high figure is unusual for a continental region being associated more with island floras. Raven & Axelrod (1978) give a figure of 47,7%, 2 125 out of 4 452 species, for the Californian Floristic Province. In South-western Australia endemism was estimated at 68%, 2 450 out of 3 637 species (Marchant, 1973), but could be up to 75–80% as genera are enlarged in new revisions (Hopper, 1979).

The impressive nature of the endemism in the Cape Flora is twofold; first is the large number of endemic species, but second and perhaps more remarkable, are the seven endemic families with one, the Bruniaceae, having as many as 75 species. These families are taxonomically distinct and some are isolated (Goldblatt, 1978) and are therefore good examples of ancient relics.

Local endemics should be treated with caution. Dahlgren (1963c) pointed out a comment made by Van Steenis that 'local endemic species loose their endemic character as soon as they are found elsewhere.' This is certainly true in the case of the Cape Flora, where more intensive collecting has brought to light new records but, on the whole, with

TABLE 2.—Endemism in the groups covered by this survey

	Genera in Africa	Endemic in Cape survey area	Species in Africa	Endemic in Cape survey area
Proteaceae (excl. *Faurea)*	12	9	393	336(85,5%)
Restionaceae	12	10	±400	386(95%)
Ericaceae-Ericoideae	24	19	826	765(93%)
Bruniaceae	12	12	75	74(95%)
Penaeaceae	7	7	21	21(100%)
Grubbiaceae	1	1	3	3(100%)
Geissolomataceae	1	1	1	1(100%)
Retziaceae	1	1	1	1(100%)
Rutaceae-Diosmeae (excl. *Agathosma)*	10	10	237	237(100%)
Aspalathus	—	—	255	251(98%)
Muraltia	—	—	115	108(94%)
Total			2235	2183(98%)

such a high degree of endemism, this is not likely to affect the overall picture to any extent.

Stebbins & Major (1965) state that discussions on endemism must involve the primary distinction between relic and newly evolved endemics. The endemism in the Cape Flora is high at species level, but also at generic and even at family level, the latter indicating the palaeoendemic nature of the Flora as a whole. It is difficult, however, to distinguish the relative age of the various centres. There is some indication that both the West Coast and Bredasdorp Centres are younger than the inland 'mountain' centres (Rourke, 1972; Oliver, 1977). Only one genus *Platycalyx* (Ericaceae) is known to be endemic to the coastal flats. This indicates that the coastal centres are neo-endemic centres relative to the 'montane' centres in which several families and genera are endemic i.e. Geissolomataceae, Roridulaceae and Retziaceae. This agrees with the known geological history of the coastal flats (Hendey, 1981). Analysis of the species covered in this survey into palaeo- or neoendemics is not possible at this stage, due to the incomplete state of our taxonomic knowledge of many of the genera.

CONCLUSIONS

There are four major phytogeographical patterns in the Cape Flora: (1) a concentration of species and diversity in the mountains of the south-western Cape with the number of species per unit area decreasing from this centre outwards, (2) a high degree of endemism to the Cape Floral Region both at specific and generic level and to a small extent family level, (3) the lack of generic endemism to the two coastal centres and (4) the existence of six centres within the Cape Floral Region which are correlated to the major edaphic and climatic systems within the region.

From an analysis of the phytogeographical patterns within the Cape Floral Region not much light is shed on the history of the Flora. Much of the present overall pattern, i.e. the delimitation of the centres and the high species numbers in the South-western Centre can be accounted for by ecological factors. The high taxonomic level of the regional endemism and the high degree of development of the centres indicate a remarkable evolutionary history *in situ* taking into account the relatively young age of the area as it exists at present and of its characteristic floral elements. This does not mean that the total area occupied by the Cape Flora did not fluctuate in the past as suggested by various authors (Levyns, 1964; Axelrod & Raven 1978), only that it has occupied the present area and has had sufficient time to develop into a very distinctive and complex flora.

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Concluding remarks and summary

J. P. M. BRENAN*

Ladies and Gentlemen, there are, I believe, two schools of thought about summaries: the first I can describe as the 'chance your arm' which consists of writing the summary before ever coming to the meeting, and be blowed to what the contributors say. The second is the 'plodding-pedestrianism' one which consists in cobbling it up as one goes along. I am a lazy chairman, and the first method had considerable attractions for me but, unfortunately, I felt I did not know enough about the subject until I had listened to the speakers, so it really was not feasible. So you have to be content with the second, and you will deduce that at the moment I am suffering from an acute attack of illness, which I can best describe as mental indigestion. I am realizing the difficulty in taking in and summing up quite so diverse a series of papers as we have heard during the past two days — quite apart from the problem of condensing the plant history of three and a half thousand million years into something less than thirty minutes. So you will have to be content with a very disconnected series of remarks, not really a summary, but a sort of magpie assemblage of things that struck me as being particularly interesting in the papers that we have heard — plus perhaps, a few critical points, too.

I suppose nobody can work or be interested in a flora as rich and diverse as that of southern Africa without being tempted to speculate and think about the origins, migration and evolution of that Flora. In giving this summary I found that the meeting was so carefully structured, and so consistent, that I had little option but to follow the chronology of the papers as they were given, dull though this method may seem.

So, in the first place, I would like to mention Professor Raven's wide-ranging keynote address. The work, of course, of Raven and Axelrod in reconciling the theories of past continental movements and plate tectonics with the distribution of floras at the present day is well known and most valuable. It has the great merits of reconciling many problems of distribution, particularly in the southern hemisphere. It reconciles trans-oceanic affinities, for example between Africa and Australia, between Australasia and South America, and also others such as those between North and South America and the well-known Afro-American amphi-Atlantic discontinuities.

If I have any sort of very mild criticism, it is that I find it sometimes difficult to accept the rain forest flora of Madagascar and the relic forest areas in East Africa as a type of the forest that covered southern Africa before past climatic changes started to take their toll. I must say, I think I would have expected more evidence in the way of relic species. I would also like to know a little bit more about how this theory explains the tremendous discontinuity, which is one of the striking features in my experience, between the flora of the Cape and the flora of tropical Africa to the north — enormous richness contrasted with comparative poverty.

I then come on to the pair of papers from Dr Knoll and Dr Anderson, dealing with the early history before the angiosperms came on the scene. I found Dr Knoll's paper a fascinating picture of life in those pre-cambrian days and, particularly interesting, in the glimpses that it gave of the rise of photosynthesis, surely one of the most spectacular events in the history of the world. I was also struck very forcibly by the extraordinary similarity of those very ancient fossil micro-organisms with apparent living relatives to-day — the similarity of Cyanobacteria and present-day stromatolites — that we were shown. I was also left with the thought that evolution must surely be proceeding at very different rates in the different groups of organisms, if those similarities are really valid. Dr Anderson took us further down the historical path from the Silurian to the mid-Cretaceous when the angiosperms came on the scene. I am not a palaeobotanist but, again, I found it a most exciting story of these successive mass rises and extinctions of conifers, psilophyta, lycopods and pteridosperms and so on. But, I am still left with the final climax in the mid-Cretaceous, when the previous groups disappeared and the angiosperms came: we can describe it, but I still feel that we are not explaining it very satisfactorily and, to my mind, it still remains that 'abominable mystery' as Darwin called it in the last century. I was struck with Dr Anderson's *cri de coeur* for more work to be done on the fossil plant material in southern Africa, for more collecting to be done, and for the results to be incorporated in a fossil flora of South Africa. Surely, an area as botanically outstandingly rich as South Africa, would find the bringing together of the evidence about its fossil history of extreme interest.

May I now come to the two papers dealing with the Tertiary history: firstly, by Professor Coetzee on the Tertiary pollen story and secondly, by Professor Boureau, dealing with the similar topic for north Africa. Again, an extraordinarily interesting part of the story of how the South African flora evolved. I was particularly struck by the presence of pollen belonging to the families Chloranthaceae and Winteraceae, and I cannot help bearing in mind the presence of living members of those families in the shape of *Ascarina* and *Takhtajania* in Madagascar at the present day and I see here support for the views put forward by Professor Raven earlier on. It is interesting to see too, in the Tertiary, that the

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Proteaceae and the Restionaceae were already abundant, which seems to me to argue for a very ancient history of the rich Angiosperm flora of South Africa.

The other point I would like briefly to allude to is the poor acidic soil on which the fynbos of southern Africa flourishes — can it really be the cause of speciation, or is it just that this happens to be a refuge for many species? I feel that sometimes we might be putting the things the wrong way round. Professor Boureau's story of the vegetation cover of the Sahara during the Tertiary, as deduced from the abundant fossil wood remains there, to me, again, was extremely interesting. I noted particularly, with a number of genera that he mentioned, although he gave them as form genera (I am deducing their affinities) — *Lovoa, Entandrophragma, Pterocarpus, Calpocalyx, Erythrophleum,* etc.; all these genera are at present quite typical of the West African forest regions; only, I think, the genus *Nipa* mentioned by Professor Boureau seems to strike a strange note. Was thus the Tertiary forest flora of the Sahara all that different from the rain forest of West Africa to-day? One would like to know more about this, and for a more critical comparison to be made. Given that composition of the Saharan forest and given the composition of the forest of that time in South Africa, there seem to be great differences which one would like to be explored and explained in a little more detail.

May I now come onto the two papers dealing with the Quaternary history of south-east and north Africa. Professor Van Zinderen Bakker gave a masterly summary of the importance of palynology and climatic changes. I was very interested in the way in which differences were emerging between the northern hemisphere and the southern hemisphere and these, I think, are very strongly reflected in the present-day floristic composition in tropical Africa, north and south of the equator. One cannot deal with large widespread genera in Africa without being struck by this remarkable difference in many savanna genera, where comparative specific poverty north of the equator contrasts with specific richness to the south.

Professor Maley described the pollen studies that he had made in the Sahara, and, again, emphasized the importance of climate, particularly, climatic fluctuations causing floras to advance and retreat; he referred also to the interpenetration of tropical and mediterranean floras, a feature which has been mentioned again by Professor Quezel this morning in relation to the present day. Dr Vogel was trying to analyse past climatic changes by novel means, the changes in the ratios of isotopes in a number of different substrates. I found this a fascinating story, although I think that it is still rather imprecise chronologically and there are other uncertainties of interpretation, but it is certainly a potentially powerful weapon which one hopes to see developed in the future. Mr White gave us a long and stimulating paper on how to interpret plant discontinuities — are they really relics of continuous ranges or are they evidence of long-distance dispersal? This is, of course, a matter of long standing argument among plant geographers. Certainly, I feel that the importance of accidental long-distance dispersal has been inadequately assessed. Before Christmas, I was in the Hawaiian Islands whose flora, highly endemic, since they are volcanic islands of relatively recent origin and far distant from any land mass, must have been exclusively recruited by long-distance dispersal except for those plants recently introduced by man. So certainly, this factor is an important one. One can argue about individual cases, but I think that Mr White's paper was an important corrective to certain trends in phytogeographical thinking. I find it difficult, however, to accept the theory of long-distance dispersal for all instances: I am, for example, rather unconvinced that *Hymenaea* drifted across the Atlantic and somehow landed up in Madagascar. It may be that it's been extinguished on the mainland continent of Africa in the intervening areas but, nevertheless, I feel that one has got to look at each case critically. But, certainly, the other point that he made about geographical speciation is, in Africa, a very important one.

Professor Werger dealt with the interrelationship of vegetation and plant communities to history. I found his paper extremely stimulating, particularly the ideas he put forward about the correlation of climate, rainfall and temperature with aberrant vegetation types. I am not entirely convinced that we are always correct in looking at islands of vegetation outside their normal distribution areas as evidence of past climatic changes; may not these be normal features of an advancing vegetation type or could they not occasionally be normal indicators of an ecotone boundary? I am putting forward these questions as they represent doubts in my own mind. Sometimes the answer is clear, but sometimes I feel it is not.

Professor Quezel's paper on the origins and evolution of the north African Flora, with all its complexity of different phytogeographical elements, again interpenetrating as we have heard, was a fine contribution. I was interested to see his mention of a northern tropical dry element, common to north Africa and north-western America, of which I think genera such as *Rhus, Cleome, Vitex,* etc., might be considered examples. I just wonder, however, whether it is right to consider that as a north African/north-west American element, but rather as an ancient relic existing in many dry areas in the world. Certainly, *Cleome* is typical of dry areas throughout Africa and also exists in other continents and I suspect the same thing could be said of other genera. Whatever one calls it, I think it is a component in the African flora of great importance in interpreting its history, and I would suggest that even a genus such as *Acacia* may be a member. I would also like to emphasize what Professor Quezel said about the mountains in the Central Sahara as possible pathways of migration for species and genera from north to south. One cannot but speculate about the presence of *Erica arborea,* for example, on the mountains in Malawi without wondering how on earth it got there; certainly a route from the Mediterranean across the mountains of the Central Sahara would seem a feasible theory. Conversely, one cannot help also speculating about whether perhaps the species of *Erica* with which we are familiar in Britain and northern Europe may not really be northern outliers of the fynbos which have somehow reached there by some such route as that. The mention of the Canaries and their richness which has come up again in discussion was also significant and I am mindful of their effect as a possible source of flora of the east African mountains. I am aware of course of *Canarina*, that endemic genus which jumps from the Canary Islands to Ethiopia and then down to east Africa, and I think that *Sibthorpia* is another genus in that group.

Later this morning we heard papers on the phytogeography of individual groups, particularly the ferns by Professor Schelpe and the grasses by Dr Clayton. Professor Schelpe's paper was a healthy corrective to our preconceived ideas that fern spores must be able to get everywhere, and I was fascinated by his examples both of narrow endemics and discontinuous distribution. It does seem very strange that one should get amphi-atlantic distributions such as that of *Woodsia montevidensis* and, the question that arises in my own mind after hearing this is, why should these endemisms and discontinuities occur? Surely the clue to these must be in the ability of spores to travel long distances, their ability or inability to survive low temperatures, and their ability or inability to colonize the substrates on which they land, and the same applies to the subsequent prothalli. It seems to me that this could be a most interesting field for precise experimental work and that we might then well be on the way to explaining with certainty just why these strange phenomena occur.

Dr Clayton described the way in which he has interpreted the distribution of grasses on a world-wide scale in relation to the history and evolution of the African flora. The way in which his differential analyses of the distributions of tribes, genera and species revealed the way in which the oceans become a progressively greater barrier to distribution, is to be specially noted. I think that similar results will be obtained from many other big families. His conclusion that the grass flora of Africa is almost exclusively palaeo-tropical is in accordance with my own conclusions for Leguminosae. I have found that the American element, in doing a generic analysis of the tropical African Leguminosae, a comparatively unimportant one. The only point of criticism I would make is his theory that the Camerouns Mountain may have acted as a barrier to migration between the two sub-kingdoms (which he correctly defined in relation to West Africa). I have been in that area myself and I found that the barrier or boundary, seemed to be a good deal to the west of Camerouns Mountain — rather in the Cross River area.

Finally, I must come to Mr Oliver and his collaborators' paper, on the distribution maps of Cape endemics. I must, most warmly, congratulate him on the very careful painstaking work, represented by these maps. They look simple when displayed on a screen but, my goodness, the amount of detailed collation, detailed patient examination of specimens and of maps they represent, is tremendous, but their source is going to be as a quarry from which one can obtain stones for building the structure of the distribution and history of South African taxa — something which I am sure most urgently needs to be done.

I suppose that I go away from this meeting with a feeling of tremendous gratitude to all the speakers and contributors. They have certainly given me a very great deal to think about. I think more importantly — and I think that this is perhaps one of the main functions of a Symposium such as this — they have indicated the problem areas of the future and there is where I think our task now lies — to continue the work so ably outlined during these past two days — to try and fill in some of the gaps. Well, I personally am willing to take small bets that this theme or something following it on is going to be a continuing subject for future AETFAT Conferences and that it is going to figure on the programme for the next one. Thank you very much Ladies and Gentlemen, for your forbearance.

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Palynological evidence for vegetation patterns in the Transvaal (South Africa) during the late Pleistocene and Holocene

L. SCOTT*

ABSTRACT

Palynological evidence relating to the nature of Late Quaternary vegetation types and plant migrations in the Transvaal is briefly summarized. It is suggested that, after an early temperate, relatively moist phase and a subsequent relatively dry phase lasting until about 25 000 yr B.P., a vegetation-type with ericaceous elements developed. It resembled belts presently occurring above the treeline and was possibly widespread over the plains of the Transvaal during the last glacial maximum period. In the central parts of the province, warm semi-arid savanna subsequently expanded during the early Holocene and was followed by a more broad-leafed type of woodland in the late Holocene. This change probably resulted from slightly wetter and, at times, also slightly warmer and cooler conditions.

RÉSUMÉ

PREUVE PALYNOLOGIQUE DE L'EXISTENCE DE TYPES DE VÉGÉTATION AU TRANSVAAL (AFRIQUE DU SUD) PENDANT LA DERNIÈRE PÉRIODE DU PLÉISTOCÈNE ET L'HOLOCÈNE

La preuve palynologique relative à la nature des migrations de plantes et des types de végétation à la fin du Quaternaire, au Transvaal est brièvement résumée. Il est suggéré qu'après une phase d'abord tempérée et relativement humide et ensuite une phase relativemant sèche perdurant jusqu'à environ 25 000 ans B.P., un type de végétation avec des éléments éricacés se développa. Il ressemblait aux étages qui se rencontrent actuellement au dessus de la ligne des arbres et étáit sans doute étendu sur les plaines du Transvaal durant l'apogée de la dernière période glaciaire. Dans les parties centrales de la province, des savannes chaudes semi-arides s'étendirent ensuite durant le début de l'Holocène et furent suivies par un type de forêt claire à feuilles plus larges. Ce changement résulta probablement de conditions légèrement plus humides et, à certains moments, aussi de conditions légèrement plus chaudes et plus froides.

INTRODUCTION

The purpose of this paper is to reconstruct the vegetation pattern of the Transvaal during the Late Quaternary by means of results obtained from pollen analyses of spring and other deposits and to assess the possible implications concerning migration and evolution. Marked climatic changes are reported to have occurred all over the world during the Pleistocene period and it is believed that, as elsewhere, these events had a major influence on the composition of the vegetation in Southern Africa. Up to now we have very little evidence of the nature of the Late Pleistocene vegetation types in the interior of the subcontinent. The important pollen diagram from Florisbad in the Orange Free State (Van Zinderen Bakker, 1957) which shows a change from a more karroid to grassland vegetation during the Late Pleistocene, is at present difficult to interpret in view of new age determinations (Rightmire, 1978) which show that the deposits are much older than previously believed. The pollen diagram from Aliwal North, Cape Province (Coetzee, 1967) only represents the terminal Pleistocene and early Holocene vegetation which developed after the amelioration of the full 'glacial' climate. Except for the oldest zone, the reconstructed vegetation does not differ widely from the present type which is transitional between karoo shrubland and grassland.

The framework for the present reconstruction was derived from pollen cores from organic and peat deposits of which the Wonderkrater thermal spring site, situated in the bushveld savanna of the low central plateau in the Transvaal (Fig. 1), is the most important. Details concerning the vegetation at Wonderkrater and large-scale pollen diagrams are presented by Scott (1982a). In the present paper, only idealized pollen diagrams (Figs 3 & 4) and a brief summary, compiled from data of four pollen profiles, are presented in order to demonstrate more clearly, changes in the environment. Supporting data from other sites in the region such as Rietvlei, Moreletta River, Scot, and Tate Vondo (Fig. 1), are

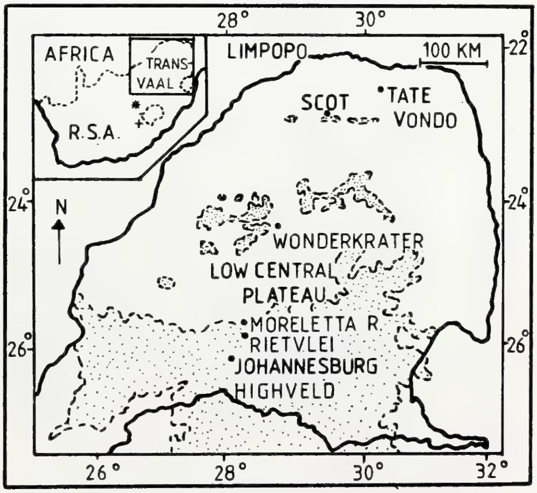

FIG. 1.—Locality map. Shaded area above 1 500 m. * = Florisbad. + = Aliwal North.

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also mentioned briefly. A study of the physiography, the climate and vegetation together with the results of 25 modern surface pollen samples from various vegetation types serve as a basis for the palaeoecological reconstructions (Scott, 1982a). The fossil pollen types and their significance in these reconstructions are described by Scott (1982b).

The pollen was extracted from the organic and peat deposits by means of standard palynological techniques mainly employing digestion in 10% KOH and mineral separation with $ZnCl_2$-solution (S.G. ±2). Eighteen relevant ^{14}C age determinations of various deposits were carried out by Dr J. C. Vogel of the CSIR, Pretoria.

THE POLLEN EVIDENCE AND INTERPRETATIONS

Micrographs of the most important indicator taxa are presented in Fig. 2. The pollen diagrams (Figs 3 & 4) from Wonderkrater show the regional pollen (A) which is made up of important AP (arboreal pollen) and NAP (non-arboreal) in the so-called pollen sum (Faegri & Iversen, 1964) and the total pollen composition (B) which consists largely of local elements. The regional palaeoenvironmental conclusions are based on the former and the percentage values mentioned below refer only to the pollen sum.

The earliest pollen zone (W1 in Fig. 3) which formed earlier than 30 000 yr B.P. consists of pollen assemblages differing widely from those produced by the present woodland type which falls within the area of Acocks's (1953) Sourish Mixed Bushveld (veld type 19). In total, the AP (arboreal pollen) is higher than in the present spectra. AP-taxa which are of importance are *Podocarpus* (≤34%), Oleaceae (≤14%) and Combretaceae (≤15%), whereas the modern pollen sum has lower AP-values consisting mainly of Combretaceae (≈6%), *Euclea* (≈6%), Tarchonantheae (≈ 5%) and relatively high numbers of NAP, especially Compositae (≈ 50%). Zone W1 is therefore thought to represent a relatively more mesic woodland on the plains and the high numbers of *Podocarpus* suggest that the montane forests in the nearby Waterberg were more extensive. The presence of *Kiggelaria* pollen (≤23%) supports the idea of wetter conditions. In general, the occurrence of small numbers of macchia elements suggests slightly cooler conditions than at present. The next zone (W2) shows a gradual decline in the numbers of AP, especially in *Podocarpus* pollen (≤10%), whereas Tarchonantheae (≤18%) and Capparaceae (≤14%) increase. This zone appears to indicate a change to a drier more open type of savanna. Zone W3 represents a short interval when *Podocarpus* (56%) dominated the pollen sum. The significance of this event is not clear. Zone W4 shows another important change in the diagram. Here the arboreal pollen content is even lower than in W2, consisting of *Podocarpus* (≤10%) and *Myrica* (≤26%). The NAP, which is important, consists of elements such as various Compositae, especially *Stoebe*-type (≤26%), and also smaller but persistent numbers of macchia elements such as Ericaceae, *Passerina* and *Cliffortia*. The reconstructed vegetation compares best with present types occurring above the treeline in the Drakensberg at altitudes of more than 1 000 m higher than Wonderkrater (1 100 m altitude). Therefore an average cooling of around 5−6°C is suggested. This cold phase corresponds with the last glacial maximum period recorded roughly between 28 000 and 14 000 yr B.P. elsewhere in the world.

The suggested lowering of vegetation zones by about 1 000 m would imply that cool open grassland or shrubland must have occupied most of the plateau above ±1 000 m. Preliminary findings from Pretoria and Venda also provide tentative support for a lowering in the vegetation belts such as is suggested by Zone W4 and may help to show that open vegetation was widespread. In those from Pretoria, open grassland or shrubland pollen with *Stoebe*-type and small numbers of indicators like Ericaceae and *Passerina* are recorded in current palynological studies of stream deposits in the Moreletta River (Fig. 1). Although no age for these layers is available, they are likely to be of Late Pleistocene or early Holocene age as they belong to the lower section of a ±50 cm layer of gray clay underlying a 20 cm peat layer with terminal age of ±5 220 yr B.P. (Verhoef, 1972). Spectra suggesting fairly open vegetation are also recorded from peats of ±2 m depth at Tate Vondo in Venda. Grass pollen is dominant and other NAP includes Ericaceae and *Passerina*. The AP consists mainly of *Podocarpus*, and also of some Combretaceae and *Myrica*. The results of current ^{14}C dating will help to determine the age of these spectra. Although it is not certain at this stage whether a vegetation type from above the treeline is represented, these results together with the data from the Moreletta River could eventually support those from Wonderkrater and help to demonstrate that the lowering of the treeline in the Late Pleistocene was quite widespread. Open vegetation could have extended as far north as Zambia in the present miombo woodland of 1 400 m altitude where there is tentative evidence for a more open vegetation in the form of a 22 000 yr old pollen sequence (Livingstone, 1971). This 5 m profile is dominated by grass pollen and below 0,5 m depth has fair numbers of *Podocarpus, Olea* and *Myrica* as the main AP component and shrubs such as Ericaceae and *Cliffortia* as NAP. Livingstone is, however, understandably cautious about his interpretation of this profile and did not provide a definite vegetational reconstruction.

At the end of the Pleistocene, climatic amelioration took place while Zone W5 at Wonderkrater was deposited (Fig. 4). The NAP, especially Chenopodiaceae (≤48%), is still very prominent, but there is a marked reduction in the percentages of macchia types while semi-arid woody elements reappear. The spectra of Zone W5 seem to represent an open dry savanna. During the next zone (W6), the Capparaceae (≤21%) and Tarchonanthaeae (≤25%) expand, while *Podocarpus* and Proteaceae pollen grains virtually disappear from the sequence. Very similar modern pollen spectra are recorded from the present warm Kalahari Thornveld (Acocks, 1953, veld type 16) of which the nearest small patch occurs

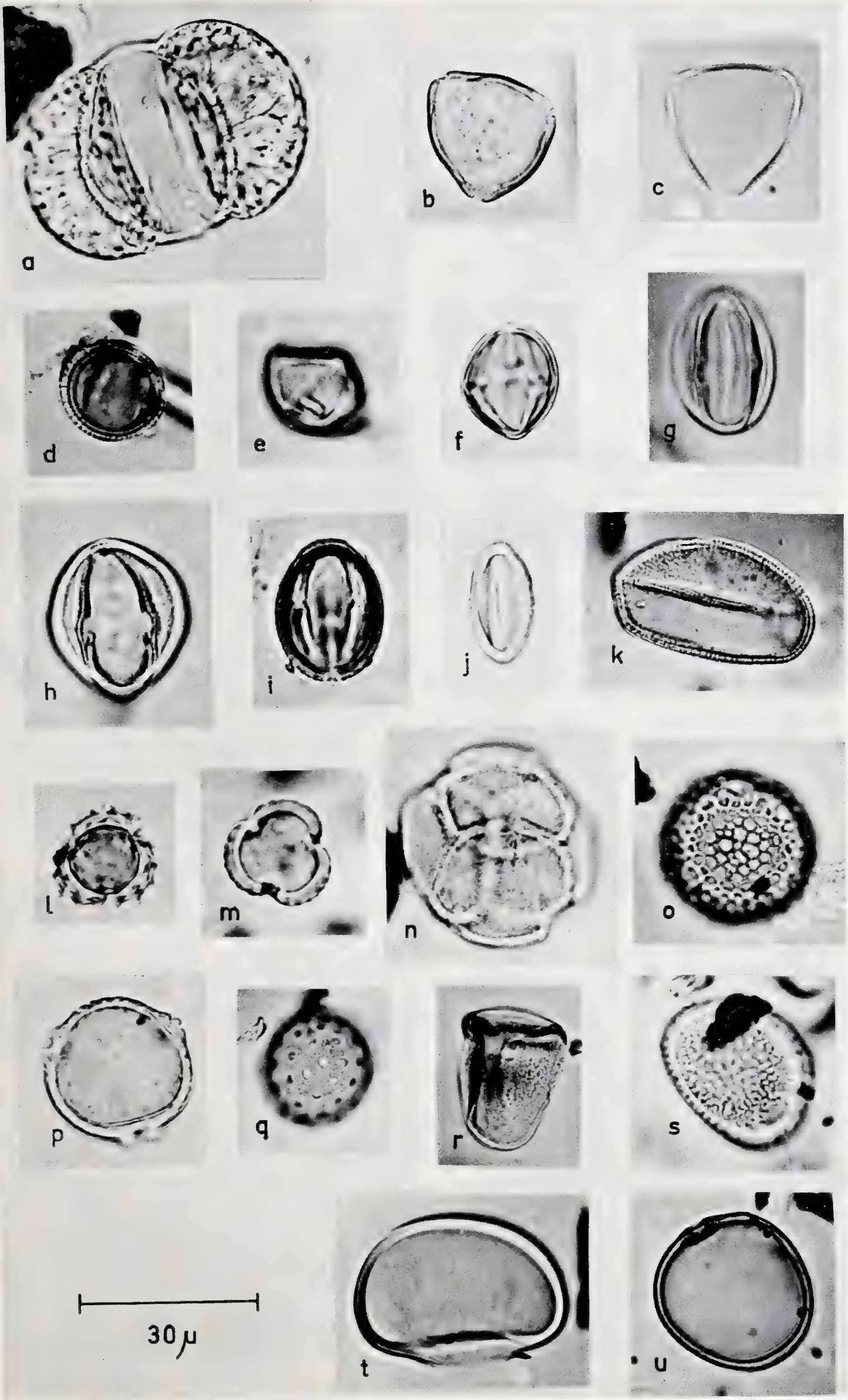

FIG. 2.—Some important fossil palynomorph types from Quaternary deposits in the Transvaal: a, *Podocarpus;* b, *Myrica;* c, Proteaceae; d, Oleaceae; e, *Burkea;* f, *Euclea;* g, Combretaceae; h, *Spirostachys;* i, Tarchonantheae; j, Capparaceae; k, Liliaceae; l, Compositae; m, *Stoebe*-type; n, Ericaceae; o, *Passerina;* p, *Cliffortia;* q Chenopodiaceae; r, Cyperaceae; s, *Typha;* t, Fern-spore; u, Gramineae.

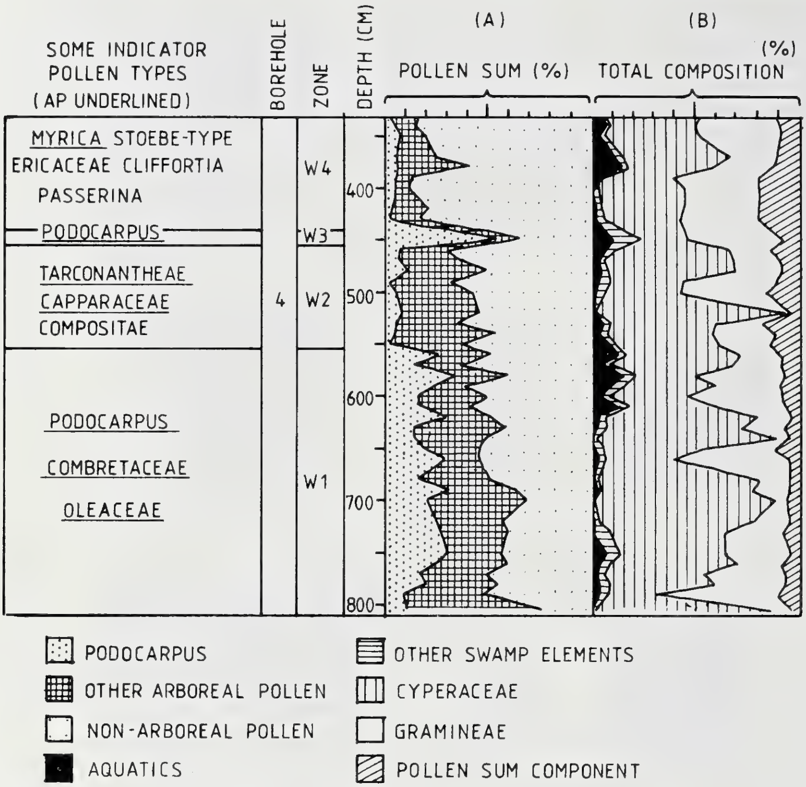

FIG. 3.—Pollen diagram of Late Pleistocene peat deposits from Wonderkrater (adapted from Scott, 1982a).

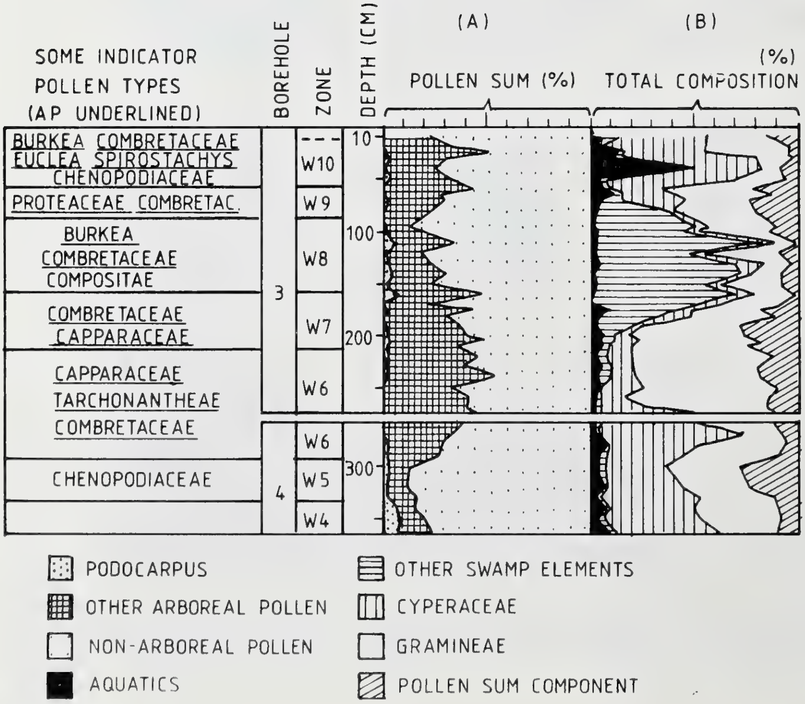

FIG. 4.—Pollen diagram of Late Pleistocene and Holocene peat deposits from Wonderkrater (adapted from Scott, 1982a).

about 100 km SSW of Wonderkrater around Pienaarsrivier Station. It is therefore possible that a similar kind of bushveld occupied a wider area and reached as far north as the foot of the Waterberg. In the next zone (W7), Combretaceae (≤18%) become important, whereas the Capparaceae and Tarchonantheae decline somewhat. Oleaceae and Proteaceae also return in small numbers and support the conclusion of a swing to slightly wetter conditions. In the next zone (W8), the AP shows a decline while NAP, especially Compositae (≤89%), becomes prominent. These spectra show a resemblance to modern surface pollen samples from upland woodland types and therefore possibly represent a more open, slightly cooler vegetation. The same kind of change also occurs around this time in a pollen sequence from the north of the Soutpansberg at 'Scot' (Scott, 1982). In the next zone (W9), bushveld pollen increases again and Combretaceae (≤16%) and Proteaceae (≤12%) become prominent. Comparison of these spectra with a surface spectrum from just north of Warmbad representing Sour Bushveld (Acocks, 1953, veld type 20) and dominated by *Faurea saligna,* shows strong similarities and suggests that it again became warmer, while slightly more humid conditions than at present still persisted. It is possible that this zone is coeval with an event recorded in the southern Transvaal highveld when a temporary expansion of the woodland occurred over the northern parts of the plateau at Rietvlei (Scott & Vogel, in preparation). However, this expansion might also have occurred earlier, coinciding, perhaps, with the deposition of the slightly mesic Zone W7 or W6b at Wonderkrater. Current ^{14}C-dating of the Rietvlei profile will throw more light on this occurrence. The nearby Moreletta River pollen sequence (in preparation), however, suggests that a marked increase in the trees of the region occurred some time after 5 220 B.P. The present savanna at Wonderkrater seemed to have developed in the youngest zone (W10) during the last 1 000 yr B.P., although there are signs that *Burkea* (≤25% pollen) was temporarily more important during this phase. The only evidence for human presence is found in the form of traces of *Zea* pollen late in the development of Zone W10.

DISCUSSION

It can be concluded that large-scale migrations of the vegetation types as suggested by pollen evidence were caused by climatic oscillations. It is difficult to estimate to what extent vegetation units migrated as a whole, but it seems likely that at certain times when new conditions arose, new combinations of species were present. For instance, Zone W2 combines elements like Capparaceae, Tarchonantheae and Combretaceae, with fair numbers of *Podocarpus* and smaller numbers of *Myrica, Kiggelaria* and macchia pollen. It is believed that the past environment in this case required a combination of temperature and moisture conditions (probably within the cooler temperate, dry sub-humid range) with a particular wind, frost and seasonal rainfall pattern which probably does not occur anywhere in Southern Africa at present. In view of the persistent oscillating nature of climatic conditions, it also seems reasonable to hypothesize that a vegetation type like the grassland with macchia-type shrubs suggested by Zone W4, was a more important part of the Quaternary scenery in Southern Africa than at present. Similarly, it will possibly be shown in future that other ecosystems like the karoo or fynbos vegetation types were more extensive during certain periods in the past. The expansion of karoo in the Pleistocene has in fact already been suggested by the pollen diagram from Florisbad in the O.F.S. (Van Zinderen Bakker, 1957).

In conclusion, the Late Quaternary record in the Transvaal seems to show a constantly migrating vegetational system but, as far as evolution of new taxa is concerned, no sign of it can be detected palynologically over this relatively short time interval. The method can, by its nature, not show evolutionary changes in plants, but only the appearance or disappearance of pollen taxa in the fossil record. Evolution of new pollen taxa only becomes noticeable over a longer time sequence ranging into the Tertiary. The modern macchia in the Cape Province evolved during the Tertiary together with the considerable and more lasting cooling of the climate in the Miocene (Coetzee, 1978). Before this cooling, the vegetation in the Transvaal region must also have been more tropical, but at this stage any fossil evidence of its nature is lacking.

ACKNOWLEDGEMENTS

I wish to thank Professor E.M. van Zinderen Bakker for allowing me to examine samples which he collected from the Moreletta Spruit and also Dr B. de Winter for sending me peat samples from Tate Vondo which he received from Mr M.T. Lingér of the Venda Herbarium.

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Le bois petrifies de la plaine de la haute Rusizi (Burundi)

M REEKMANS*

RÉSUMÉ

Les recherches paléontologiques dans le domaine de la botanique en Afrique centrale sont encore très fragmentaires. Au Burundi, en dehors des très classiques et abondants stromatolithes du Mosso (sud du pays), Sah (1967) a signalé la présence de débris végétaux dans les sédiments fluviolacustres de la plaine de la moyenne Rusizi. Ces fragments n'ont jamais été identifiés mais un examen des grains de pollen présents dans les couches sédimentaires de même âge, a permis de préciser certaines caractéristiques de la végétation et du climat qui régnait dans la région au Néogène supérieur.

En novembre 1978, nous avons découvert dans le nord-ouest du Burundi un gisement de troncs pétrifiés de taille assez exceptionnelle. Ces fossiles avaient été mis à jour quelque temps auparavant, lors de la mise en exploitation d'une petite carrière de cailloux roulés auxquels ils se trouvaient mêlés. Le gisement comportait 4 troncs dont deux de grande taille: longueur: 1 m; diamètre: 90 cm; poids: plus de 1 000 kg.

Un premier examen macro-puis submicroscopique sur éclats nous avait permis de reconnaître une structure anatomique rappelant celle de certains fossiles décrits du Kivu (Zaïre) et appartenant à la famille des Caesalpiniaceae.

Des échantillons ont été envoyés à Tervuren (R. Dechamps) et à Liège (Mme Demaret). II ressort de leurs observations et études en commun que les troncs en question appartiennent au genre *Julbernardia* et probablement même à l'espèce *J. globiflora.* Leur âge serait de l'ordre de 1 200 000 ans environ.

Depuis lors, d'autres troncs ont été mis à jour (au moins dizaine). D'un premier examen que nous avons fait, il ressort qu'ils possèdent une structure très différente de celle des spécimens précédents. Des échantillons ont été envoyés à Tervuren et à Liège pour étude et les conclusions des spécialistes devraient nous parvenir très prochainement.

ABSTRACT

THE DISCOVERY OF PETRIFIED FOSSILS IN THE HIGH RUSIZI PLAIN (BURUNDI)

Palaeobotanical research in Central Africa is still very fragmentary. In Burundi, apart from the very classical and abundant stromatolites of the Mosso (in the south of the country), Sah (1967) has indicated the occurrence of vegetal debris in the fluviolacustrian sediments of the mid-upper Rusizi plain. These fragments have never been identified, but a study of the pollen grains found in sedimentary layers of the same age has revealed some features of the vegetation and of the climate prevailing in the Upper Neogene period.

In November 1978 we discovered in north-western Burundi a deposit of petrified trunks of exceptional size. These fossils had been exposed a short time previously when a small quarry was established. The deposit contained four trunks, two of which were large: length, 1 m; diameter, 90 cm; weight, more than 1 000 kg.

Initial macro and submicrospic examination of fragments showed an anatomical structure similar to the structure of some fossils described in Kivu (Zaïre) and belonging to the family Caesalpiniaceae.

Samples were sent to Tervuren (R. Dechamps) and to Liège (Mrs Demaret) and their joint studies revealed that these trunks belong to the genus Julbernardia *and probably to* J. globiflora. *Their age would be about 1 200 000 years.*

Since then, other trunks have been found (at least ten). According to our study, it is concluded that they have a very different structure from those of the previous specimens. Samples were sent to Tervuren and to Liège for further study and the conclusions from the specialists should be available very soon.

Outre les classiques stromatolithes du Mosso (sud-est du pays), on a signalé le présence, au Burundi, (Sah, 1967) de débris végétaux fossiles dans les sédiments fluviolacustres du Néogène supérieur de la plaine de la moyenne Rusizi. Comme c'est souvent le cas en Afrique, il s'agissait de fragments de petite taille, ne dépassant généralement pas quelques centimètres de long pour un poids de l'ordre de quelques dizaines de grammes seulement.

En novembre 1978, à l'occasion de travaux routiers effectués dans le secteur nord-ouest du Burundi, un premier gisement de troncs pétrifiés a été découvert dans une carrière des environs de Cibitoke (voir cartes 1 et 2). Les coordonnées géographiques de l'endroit sont les suivantes : lat. sud : 2°54, long. est : 29°07; l'altitude du site est de 1 000 m environ.

Dans ce premier gîte fossilifère figuraient 4 troncs : deux de grande taille (longueur 1 m, diamètre 90 cm, poids supérieur à 1 tonne) et deux de dimensions plus modestes pesant approximativement 300 et 100 kg environ. Tous ces troncs étaient intégrés à une couche alluvionnaire d'épaisseur variant entre 1 et 3 m et constituée de galets mal calibrés de quartz filonien, de quartzite et d'amphibolite, mêlés à des cailloux d'hématite, et englobant des blocs, parfois de grande taille — 1 m de diamètre — de calcédoine. On y observait aussi de gros blocs arrondis (altération en boule) de laves basaltiques vertes ou noirâtres. En fait, toute cette couche constitue probablement une ancienne terrasse de la Nyamagana. Elle repose sur une coulée de lave basaltique, cellulaire et fortement altéreé en une argile résiduelle verte, recouvrant elle-même soit les

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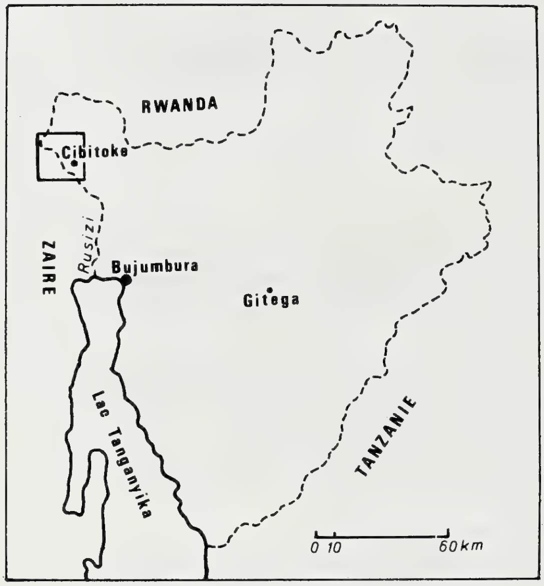

FIG. 1. — Localisation du gisement au Burundi.

dépôts essentiellement sableux d'origine fluviolacustre de la plaine de la Rusizi, soit les formations métamorphiques du socle précambien. Les dépôts fluviolacustres les plus anciens, dans cette région, datent du Plio-Pléistocène et du Pléistocène supérieur (Sah, 1967).

Le fait de trouver ces troncs pétrifiés mêlés aux cailloux roulés, ainsi que la présence de traces très nettes de fractures et de craquelures dans leur structure interne indiquent que ces arbres ont dû subir un transport. La fréquence et l'importance de ces craquelures laissent supposer que ce transport aurait été postérieur à la silicification.

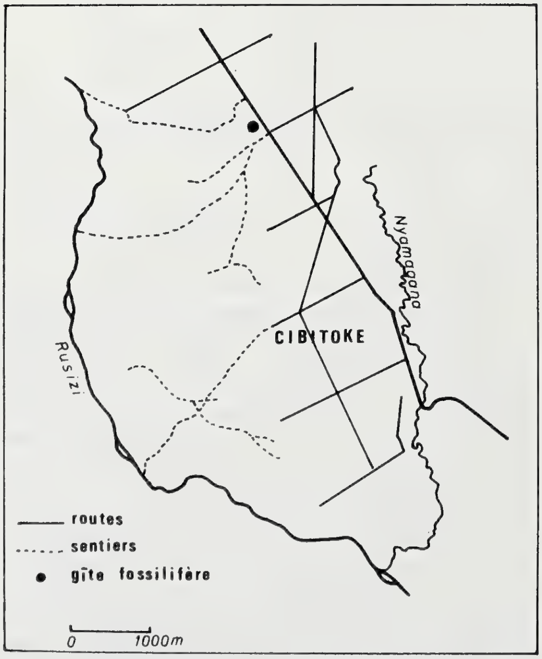

FIG. 2. — Localisation du gisement dans la region de Cibitoke.

L'imprégnation du bois (lumen et parois cellulaires) par le silice doit être mise en relation avec l'activité volcanique du Sud-Kivu, la silice colloïdale provenant soit du lessivage des roches volcaniques, soit des apports des sources thermominérales. Ces conditions sont réunies dans tout le fossé tectonique du Kivu-Tanganyika. Au Burundi plus particulièrement, les laves affleurent de façon discontinue dans tout le secteur et notamment sur une étendue de plusieurs km^2, entre la Nyamagana et la frontière rwando-burundaise (voir carte 3). Ces coulées de laves appartiennent vraisemblablement aux épanchements volcaniques du Sud-Kivu et datent de l'Eocène supérieur ou du Mio-Pléocène. Dans le même ordre d'idées, on trouve dans la plaine de la Rusizi, plusieurs sources thermales dont certaines sont encore en activité actuellement, notamment près de la frontière rwando-burundaise.

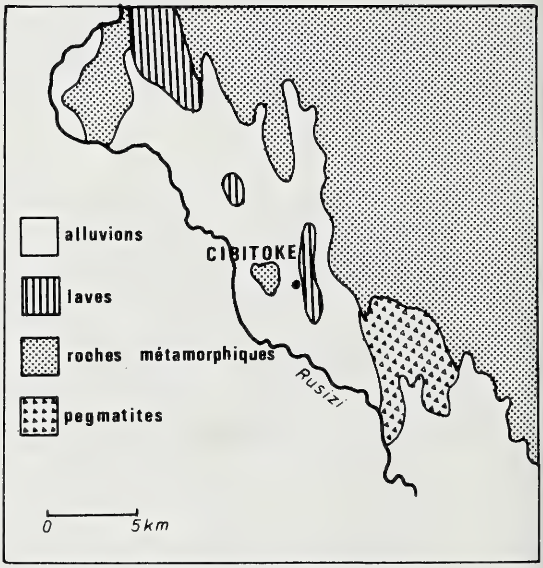

FIG. 3. — Esquisse géologique de la region de Cibitoke.

Les troncs silicifiés récoltés au Burundi ne montrent jamais les riches colorations des fossiles de l'Arizona. Généralement brun jaunâtre en profondeur, ils présentent une croûte d'altération superficielle blanchâtre. Les régions les plus propices à une étude anatomique se trouvent à 4–5 cm de profondeur; la conservation des tissus y est souvent presque parfaite.

Ces études anatomiques ont porté sur des fragments prélevés sur les deux 'gros' troncs (A & B). D'une manière générale, les structures cellulaires sont mieux conservées chez le spécimen A que chez le spécimen B.

Lorsque le plan de cassure correspond plus ou moins à une section transversale du bois fossile, les vaisseaux sont visibles à l'oeil nu et apparaissent sous forme de petites taches de la taille d'une tête d'épingle. Des lignes radiales de teinte plus claire strient la masse brunâtre du bois : elles correspondent aux rayons ligneux. Chez le spécimen B, on distingue en plus, à l'oeil nu, de fines lignes tangentielles plus ou moins longues et plus ou moins espacées.

Les observations microscopiques ont porté plus particulièrement sur les vaisseaux, le parenchyme vertical, les rayons et les fibres. Pour ce qui concerne le spécimen A, leurs caractéristiques ont permis de le rattacher au groupe des Légumineuses et, eu égard à la présence de rayons mono- à trisériés non étagés, à la famille des Caesalpiniaceae (Fairon-Demaret, Dreesen & Reekmans, 1981).

Par comparaison avec de bois des représentants actuels de cette famille, il a été possible de rapprocher l'échantillon A du genre *Julbernardia*, et même de l'espèce *J. paniculata* (Benth.) Troupin. Toutefois, les différences décelées au niveau des rayons — qui ne sont jamais bisériés dans l'espèce moderne — permettent de conclure qu'il s'agit probablement d'une espèce nouvelle qu'il est préférable dans les conditions actuelles de laisser en 'nomenclature ouverte'.

Pour le spécimen B, les caractéristiques sont celles des Meliaceae en général et du genre *Carapoxylon* plus particulièrement. Les espèces fossiles de ce genre, connues notamment du lac Mobutu Sese Seko (=lac Albert), sont très différentes de celle du Burundi, qui serait plus proche du genre Sterculioxylon, mais qui lui aussi présente des analogies très marquées avec les Meliaceae.

L'analyse des autres débris lignifiés, de plus petite taille, du gisement n'est pas terminée. De nouveaux travaux routiers ont permis la découverte de nouveaux gisements, et d'autres échantillons ont été prélevés. Leur étude, complémentairement à celle réalisée par Sah à propos des spores et des grains de pollens isolés des alluvions fluviolacustres de la plaine de la Rusizi, permettront sans doute de préciser davantage les conditions écologiques, l'évolution et les caractéristiques de la flore du Néogène supérieur dans la région, pour laquelle Sah reconnaît généralement un caractère tropical de type humide.

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The dispersal versus vicariance debate in biogeography

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ABSTRACT

Wild's 1964 study of the Chimanimani Mountain endemics is taken as an example of a vicariance model: endemics (1) are seen to have originated *in situ* from a residual fragment of an ancestral, once-continuous flora; (2) are held to present in themselves no history of major dispersal; and consequently a biogeographical intrepretation involving or presupposing their 'migrations' is not thought to be applicable. The preference Wild expressed for this model over a dispersalist model attributed to Levyns is investigated, making use of theoretical refinements developed in the dispersal vs vicariance debate within the past decade. The differences in intrepretations between Wild and Levyns appear to be unresolvable on account of their positions not being demarcated clearly enough, and the situation has not improved since then, underlining the need for attention to be given to the formulation of applicable, coherent and testable hypotheses in biogeography.

RÉSUMÉ

LE DÉBAT BIOGÉOGRAPHIQUE ENTRE LA VICARIANCE ET LA DISPERSION

L'étude de Wild en 1964 sur les endémiques des monts Chimanimani est prise comme un example d'un modèle de vicariance: les endémiques (1) sont considérées comme étánt originaires in situ *d'un fragment résiduel d'une flore ancestrale, autrefois continue; (2) sont tenues comme ne présentant en elles-mêmes aucune histoire de dispersion majeure; et par conséquent une interprétation biogéographique impliquant au pré-supposant leurs 'migrations' n'est pas considérée comme applicable. La préférénce exprimée par Wild pour ce modèle contre le modèle de dispersion attribué à Levyns est investiguée, en faisant usage des perfectionnements des théories réalisés dans le débat 'dispersion ou vicariance' de la dernière décade. Les différences dans les interprétations entre Wild et Levyns apparaissent être insolubles parce que leurs positions ne sont pas assez clairement démarquées, et la situation ne s'est pas améliorée depuis lors. Ceci soulinge le besoin d'accorder une attention plus grande à la formulation d'hypothèses applicables, cohérentes et vérifiables en biogéographie.*

This paper is concerned with a debate that took place mainly among North American biogeographers during the 1970's. The debate arose out of differing approaches and viewpoints that were in fact already causing disagreement among southern African phytogeographers in the 1960's, but there has been little attempt in this continent to clarify the issues involved, and we have much to learn from the argument that developed to the north in the past decade.

The debate among North American workers was largely sparked by members of the American Museum of Natural History, who gave support to the approach and methods of the South American botanist Leon Croizat. In several publications over the previous twenty years, Croizat had been contrasting his work with what he took to be orthodox biogeography. The latter was seen by him to have its origin in Darwin's work and to be grounded on the assumption that every taxon comes into being in a centre of origin, from which migration may occur by some means of dispersal. Yet the event of dispersal is only assumed, not demonstrated, and the means of dispersal are not specified — or are even not rigorously specifiable at all.

In a paper on African biogeography, Croizat (1968: 430) stated that 'In sharp opposition to conventional biogeography for which migration is the main problem, the (pan)biogeographic method I stand for emphasizes form-making as essentially molded by *vicariism*'. Such 'vicariant form-making' is held to follow an 'original Permo-Jurassic "radiation" ' (p. 432 & 433), with the 'establishment of Triassic and Jurassic main centres of evolution and massings' (p. 433). Fragmentation of these 'centres and massings', such as through continental drift, results in related taxa occurring on different continents 'without the vicariant taxa ever having moved from their original centres of form-making' (p. 434). Thus (p. 434), 'An ancestral group, whether plants or animals, originally distributed by "radiation" to the lands become in our geographic maps, e.g., Brazil, Nigeria and Borneo, may by subsequent, strictly local form-making yield, e.g., three different genera in each one of these lands. To assume that the origin of these genera is due to the active "migration" of one of them from, e.g., Brazil to Borneo, Borneo to Nigeria, etc., is most certainly not what competently conducted analyses of dispersal show to be true and correct'.

On a more local scale, Croizat (*in litt.*, 1965) cited a passage from Wild's study of Chimanimani Mountain endemics as being 'precisely the leitmotif of the book [*Space, time, form,* Croizat, 1962], resuming all my work'. Wild's passage (1964: 129; see also Croizat, 1968: 87) reads: 'In discussing these vicariads, it will be noted that there is no tendency towards affinities in any particular geographical direction. In different genera the nearest affinity may be with the Cape, Tanganyika, Angola, or the next geological formation in the Chimanimanis. This would indicate evolution from a flora blanketing a large or even continental area and not from a flora moving along more or less narrow lines of migration'. Wild here finds 'migration' to have no

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explanatory value regarding the Chimanimani endemics: species in this flora may originate *in situ,* and need not present any history of dispersal. They are seen to be derived from a residual piece of a 'Cape Flora, or its direct evolutionary precursor,' which 'covered a large continuous area of the African Continent up to the early Tertiary,' but which subsequently became 'very much fragmented and remained in tropical Africa only in montane areas' (Wild, 1964: 132). According to this model, Capensis endemics would also be regarded as having originated *in situ,* in this case in the south-western and southern Cape as derivatives of another 'fragment' of the widespread 'Cape Flora [in a broad sense], or its direct evolutionary precursor'. Again, these endemics themselves would not be thought to present a history of migration or dispersal, having originated *in situ.*

In Wild's study, the Zambesi and Limpopo Basins are not treated as 'barriers' to northward or southward 'migration' of species: the basins are discussed as 'intervals', as factors in the 'fragmentation' of former more extensive ranges. This contrasts with a 'migrationist' viewpoint, which tends to see such basins as 'barriers' to the spread of already-formed species. Thus in a vicariance viewpoint, 'barriers' tend to be considered as factors prior to the event of speciation; in a dispersalist viewpoint, 'barriers' tend to be considered as factors affecting species mainly *after* their origin.

Like Croizat, Wild (1968: 210) saw an incompatibility between the vicariance and dispersalist viewpoints, preferring his 'explanation' that 'the Cape Flora became very much fragmented and remained in Tropical Africa only in montane areas' to the idea attributed to Levyns (1964) of a 'migration from Central Africa to the Cape' of several 'Cape' genera. He did not, however, totally reject every idea of 'migration' and 'barriers', especially in more 'recent time' (1968: 211), and the differing viewpoints did not develop into controversy: he did not take up Cain's (1944) or Croizat's criticisms of the idea of centres of origin and dispersal, even though he quoted both authors in other contexts.

It was in the mid-1970's that a major argument developed, initiated by two ichthyologists in the American Museum of Natural History, G. Nelson and D. E. Rosen. The events can be seen as something of a palace revolution in the American Museum, which for several decades had been the centre of an influential zoogeographical school, adhering to Darwinian views of an unchanging patterning of the continents and 'that species originate in a small area and thereafter expand in range according to the efficacy of their means of dispersal' (Nelson, 1973: 315). This viewpoint had been receiving Croizat's sustained criticism, and 'the recent and stunning breakthrough of the neowegenerians' (Nelson, 1973: 314) at this time gave Croizat's criticisms a fashionable touch.

The 'breakthrough' in plate tectonics also gave positive support to Croizat's idea of vicariism. Rosen (1975: 489) characterized Croizat's 'biogeography of vicariance' as recognizing 'biotic patterns arising largely from biotic fragmentation in response to geographic change, rather than from dispersals from centres of origin'. Rosen pointed out that Cain and Croizat share several central concepts, yet he believed (1975: 490) 'it is evident that Cain failed . . . to achieve some general, synthetic approach which could give order and direction to biogeographic investigation'. Croizat, on the other hand, was held (Rosen, 1974: 289) to have developed 'a science of biogeography that depends on rigorous methods of analysis and the formation of testable hypotheses'.

A more critical appraisal of biogeographical hypotheses was given by Ball in a symposium on perspectives in biogeography published in the 1975 volume of *Systematic Zoology.* Ball stated (1975: 419), 'I believe that Croizat has contributed more than any other single person to the science of biogeography'; nevertheless, he presented a zoogeography of planarians which made use of both vicariance *and* centre of origin/dispersal models — a practical rejection of Croizat's contention that one model 'rules out the other' (Croizat, 1968: 431). Ball stated (p. 415) that 'for austral distributions I am invoking a vicariance model for the older, more primitive taxa, whereas it seems proper to talk of centres of origin and dispersal' for genera reaching the northern hemisphere after the closure of the Tethys Sea, subsequent to the family becoming disjunct in the southern hemisphere through continental drift. Ball favoured the rejection of the concept of centres of origin by Croizat, Nelson and Rosen, either separately or jointly (Croizat, Nelson & Rosen, 1974), but only if the concept was rejected 'in a restricted sense, as a necessary initial premiss of all biogeographical enquiry'. (p. 420). Similarly, 'the rejection of casual or waif dispersal as a prior basis for biogeography is, to my mind, well founded. Nonetheless it does occur' (p. 420).

Ball's paper is particularly interesting because of its expression of freedom by a North American biogeographer who has broken out of the ruling 'center of origin/dispersal paradigm' (Nelson, 1975: 493). 'For me,' Ball wrote (1975: 422), 'Croizat's contribution is one of liberation'. He believed that Croizat's ideas 'have not destroyed the realities of "dispersal as translation in space" or "centres of origin," although they have released us from their tyranny' (p. 422). He stressed, however, that 'this freedom does not relieve us of the responsibility of formulating our hypotheses properly, so that they can be refuted. Croizat failed to do this and I can detect no greater success in the writings of Rosen or Nelson' (p. 422).

The justification that Ball gives for rejecting the centre of origin paradigm 'as a necessary initial premiss of all biogeographical enquiry' is as follows: some writers hold that 'it is the ancestral populations that remain at, or near, the point of origin, and the derived forms that migrate' (pp. 419–420). Other writers 'reject this reasoning and argue that it is the derived forms that force the ancestral forms to a peripheral situation' (p. 420). It is 'difficult to decide *a priori* between these two possibilities', Ball believes. Indeed, several authors have argued that a decision of this kind cannot be made at all, because, even if the centre of origin paradigm be accepted, the centre of origin itself cannot be determined from the present range of a taxon (e.g. Udvardy, 1969: 240, 'Because of the temporal instability of the area, it is futile to search for centres of origin or dispersal within existing distribution areas.'). As will be noted later, it is important to bear this point in mind in any discussion of the 'origin' or 'migration' of the Cape Flora.

Regarding dispersal, Ball (1975: 420) observes that 'One reason for rejecting chance dispersal *a priori* as a causal factor in biogeography is that it leads to poorly formulated and usually untestable hypotheses'. Examples of such hypotheses — if they can be called hypotheses — are common enough in African phytogeography: thus, '*Dietes* probably achieved this distribution through long distance dispersal, although it is not possible to say when and how' (Goldblatt, 1978: 401–402). Of such hypotheses, Ball remarks, 'They are rational but they tell us little' (p. 422). He stresses the need for 'bold speculative hypotheses based on theories of descent . . . If the Popperian conception of science is accepted then it is largely irrelevant as to how hypotheses are derived. What matters is their formulation, consistency, predictive power, and testability, in short, the total heuristic value' (p. 422).

Did the vicariance viewpoint of Wild or the centre of origin/dispersal viewpoint of Levyns employ 'hypotheses' according to these specifications; or were the viewpoints based on mere 'narrative', as Ball termed it, telling 'a rational historical story but it calls on no laws, nor even hypotheses of relationships . . . and it enables no positive or negative predictions to be made' (Ball, 1975: 410)? If the latter is the case, then, as Ball (p. 411) observes, 'we are reduced to a non-logical comparison of the type that attempts to demonstrate that cricket is a better game than baseball. One may state a preference, but one cannot justify it logically'. Much biogeographical argument, as Ball points out, has in fact been of this kind.

Bearing all the foregoing in mind, we may now look critically at Wild's preference for his viewpoint over that attributed to Levyns. In the first place, did he have scientifically acceptable grounds for making a comparison at all, or was his preference similar to choosing between cricket and baseball?

Wild firstly satisfies Ball's requirement that the hypotheses should be 'based on theories of descent', since he considers the distribution of the 'nearest affinities' of Chimanimani endemics. The stated lack of 'any particular geographical direction in these affinities' is something that can be tested statistically. It leads by traceable logic to the inference that there is no evidence for 'more or less narrow lines of migration' (although no specifications are provided regarding the term 'narrow'). The other inference, of 'evolution from a flora blanketing a large or even continental area', is likewise logical, although ambiguity is introduced in the statement (1964: 132) that it was 'the Cape Flora, or its direct evolutionary precursor' that did the blanketing. This phylogenetic ambiguity will be found to be troublesome later. At least the hypothesis of early Tertiary period for this 'blanketing' and its subsequent fragmentation is based on a review of the geological and palaeoclimatic evidence available at the time, so this hypothesis is readily testable.

There still remains the question of how, by what movements, the early Tertiary 'blanketing' was accomplished. The blanketing could be seen as the product of Croizat's postulated 'Triassic and Jurassic main centres of evolution and massings', established after the upheavals of the Permo-Carboniferous Ice Age. The vicariance model necessarily holds that the 'radiation' which led to the establishment of these 'massings' was performed by taxa mostly ancestral to the ones now present. Theories regarding the spread of these ancestral forms at such remote times, over a geography markedly different from the present, obviously must belong to a set different from the set of theories concerned with later *in situ* diversification. Croizat (1962: 184; 1981) indeed takes this into account in recognizing alternating phases of 'mobilism' and 'immobilism'; major phases of mobilism are seen to be initiated by environmental 'revolutions' such as the Permo-Carboniferous and Plio-Pleistocene Ice Ages, separated by periods of more stable environment with consequent immobilism and vicariation or 'local form-making' (Croizat, 1968: 434). Wild does not attempt to describe events during the phase of largely pre-Tertiary mobilism — no firm suggestions are made as to how, and by what movements, the early Tertiary 'blanketing' came about; and little is put forward as testable hypothesis by Croizat regarding mobilism or radiation in southern Africa. This lack of firm hypothesis is important to bear in mind when considering the views of Levyns, with which Wild states disagreement.

It may be noted that Levyns (1964) starts from a position very similar to that of Wild. Writing on primitive species found in upland outliers of the Cape Flora in central Africa, she states (p. 91), 'It is difficult to avoid the conclusion that they represent relics of a once widespread flora, forced by changes of climate to take refuge on mountains which alone provide conditions necessary for survival.' From the Cape genera she reviews, however, she finds (p. 94) the repeated 'picture of a genus arising in the north, leaving behind scattered records of its journey southwards, and finally undergoing intensive speciation in the south-west'. Thus, in the Persoonioideae (Proteaceae), 'The paths are marked by relics of the two oldest genera, *Faurea* and *Protea*' (p. 93). This 'picture', not of a 'once widespread flora' but of genera 'arising in the north' and then proceeding on a 'journey southwards', was seen by Wild to be incompatible with his picture of *in situ* evolution by isolated fragments of a formerly continuous flora.

If Levyns's 'picture' allows for the occurrence of evolutionary change during the course of migration southwards, then the differences between her interpretation and that of Wild finds a parallel in the differences between the 'phylogenetic biogeography' of Hennig and Brundin (Brundin, 1981) and the 'vicariance biogeography' of Croizat, Nelson and Rosen. The differences between these two schools have recently been discussed in some detail at a symposium (Nelson & Rosen, 1981), and the arguments cast some potentially clarifying light on the 'origin of the Cape Flora' debate.

Brundin, the author of classic work on austral vicariance patterns in chironomid midges, states (1981: 95) that phylogenetic biogeography is the 'biogeographical implication' of Hennig's phylogenetic systematics (Hennig, 1966), providing an 'alternative model' to the Croizat-Nelson-Rosen vicariance model. In complete contrast to Croizat, Nelson and Rosen, dispersal is taken to be of fundamental importance, 'dispersal' in this context being defined as 'the stepwise progression in space by marginal portions (border populations) of the gross population of a species' (Brundin, 1981: 107). This peripheral spread is taken to be the result of environmental change, the 'disappearance of a former barrier' (p. 107). Such geographical progression can be accompanied by phylogenetic progression: 'Dispersal by an incipient ancestral species followed by isolation and speciation will give rise to peripheral apomorphy [phylogenetic advancement], not to peripheral plesiomorphy [conservatism]' (p. 108). If such dispersal occurs, 'then the comparatively plesiomorphic species or group will be closer to the initial range of the common ancestral species than the apomorphic sister species or sister group' (p. 109). Therefore, in contrast to Croizat's idea that 'form-making' occurs not at a time of 'mobilism' but of 'immobilism', the Hennig-Brundin 'progression rule' directly couples 'form-making' and 'mobilism'; and further, makes a prediction that more primitive forms will be found in the 'initial range'.

In the context of southern African phytogeography, the Hennig-Brundin model would see Capensis as the endpoint in a geographical and phylogenetic 'progression' from an ancestral range in central Africa, and not the result of *in situ* evolution in an already-dispersed and now immobile and fragmenting 'blanketing'. Yet there is, of course, no logical inconsistency in applying *both* models to Capensis: the 'journey southwards' envisaged by Levyns could involve some phylogenetic progression, which would then be taken further by *in situ* evolution once populations were established in the south-western Cape.

Unfortunately, there seems little indication that Levyns took a clear position in this respect. In concluding her 1964 paper she stated (p. 103) that 'much of the Cape Flora had its origin north of its present station and that it migrated southwards'; but she did not specify whether the migrating 'it' was intended to refer to the present assemblage or to some 'evolutionary precursor', to use Wild's phrase — although, as already noted, Wild himself was ambiguous on this phylogenetic point. Levyns observed (p. 97) that 'it is not impossible that in the course of evolution some species may have been transferred from one community to another . . . It is not difficult to visualise a descendant of this adaptable species ultimately becoming a member of a flora quite different from that in which it originated'. This suggests some idea of evolutionary change occurring *during* the course of migration, conforming to some extent with Hennig's progression rule. Yet another migratory mechanism is considered later (p. 105), namely that 'The northward movement of Africa as a result of continental drift would result in changes of climate of the very type needed to explain the southward movement of floras'. This suggestion, notably modern for its time, does not shed light on exactly what the 'stream of migration' to the Cape was considered to consist of phylogenetically. But it does suggest some point in time for the event, and in another paper (Levyns, 1962: 8) a corresponding point in time is suggested: since 'certain elements of the montane flora of Madagascar clearly belong to the Cape Flora and have their nearest relatives on the mountains of East Africa . . . the Cape Flora must have been in existence before the separation took place'. This time would be mid-Cretaceous to early Tertiary, as reviewed in Axelrod & Raven (1978). Another piece of evidence that Levyns (1964: 92) brings forward regarding time is the absence of pollen grains of Ericaceae from the Knysna lignites, pointing to the conclusion that by the probable time of early Tertiary, 'the Ericaceae had not at that time arrived in southern Africa'.

It may be noted that the time suggested by her for the 'stream of migration' is not markedly different from the time suggested by Wild for the 'blanketing' of the Cape or pre-Cape flora. One wonders whether Wild and Levyns were in fact talking at least partly about the same thing from their different viewpoints; yet because their positions were not demarcated sufficiently clearly — Levyns's in particular has a strong admixture of 'narrative' in Ball's sense — the matter remains unresolvable. This highlights the need that Ball (1975: 422) stressed regarding biogeographical hypotheses: 'What matters is their formulation, consistency, predictive power, and testability, in short, the total heuristic value'.

The aim of this paper is not to argue for the correctness of either a vicariance or a dispersalist viewpoint in the context of African biogeography. In this complex field of study, both are applicable, both can yield testable hypotheses, as Ball showed in the case of planarians. Further, vicariance and dispersal can be seen as 'each other's corollaries' (Brundin, 1981: 130) in the viewpoint of phylogenetic biogeography. It is much to the credit of Levyns and Wild that they both recognized the importance of continental drift and its vicariance implications for southern floras at a time when the weight of biogeographical opinion outside Africa was against the idea. Thus Levyns was free of some of the major constraints of the centre of origin/dispersal paradigm, even if she evidently took other aspects, including a search for 'paths of migration', to be — as Ball (1975: 420) put it — 'a necessary initial premiss of all biogeographical enquiry.' A consequence of this programming is the tendency to overlook or underestimate the signs of extensive *in situ* evolution of endemics, to which interpretations involving 'paths of migration' are simply inapplicable.

It seems fair to say that neither the dispersalist nor vicariance model has gained further status as a scientific hypothesis at the hands of subsequent writers on the major features of African phytogeography. Leach (1976) has pointed out errors in Croizat's (1965, 1967, 1972) treatment of African *Euphorbia,* and the historical phytogeography of this 'frighteningly large genus' (Leach, 1976: 17) still awaits a fresh review. The different viewpoints of Wild and Levyns received coverage but no elaboration in Werger's *Biogeography and ecology of southern Africa* (Killick, 1978: 520–521). An attempt at rigorousness within the centre of origin/dispersal paradigm was recently made by Holland (1978) in his study of the genus *Aloe.* An 'index of dispersal' based on values reflecting 'the greatest variety of forms and a concentration of the more primitive of them' (p. 222) is used to identify the 'centre of origin of a taxon'. Zimbabwe is shown to have the greatest diversity and highest concentration of primitive species of aloe as judged by vegetative characters, and it is held (p. 224) that 'the ancestral aloes first appeared in southeast Africa some time before land connections with Malagasy were severed in the late Mesozoic — early Tertiary. From there they dispersed along the rising highlands of eastern and southern Africa . . .'. Holland perceptively states (p. 224) that 'Everything depends on the ordering of the aloes in an evolutionary sequence, and it is by no means certain that the proposed system is the most efficient'. His analysis and resulting biogeographical thesis to some extent resemble the techniques and the results of the phylogenetic biogeography of Hennig and Brundin, and their rigorous procedures could well be tried by African phytogeographers.

At present the tendency is more for dispersalist models to be presupposed or adopted unthinkingly, or else be used as a 'waste-basket category': if no definite hypothesis to account for a feature of distribution emerges, then the 'explanation' must be some kind of dispersal. This is unfair to the concept of long-distance dispersal, which certainly can stand as a testable and heuristically useful hypothesis in many particular cases (e.g. Udvardy, 1969 & 1981; Pielou, 1979), and which has been recognized by many biogeographers as being one of two basically different processes by which the geographical isolation of populations occurs; range subdivision and barrier-crossing dispersal. As summarized by Haffer (1981: 390), the two processes are : '(1) fragmentation (sub-division, "vicariance") of a pre-existing continuous species range, or (2) crossing of a pre-existing barrier by some dispersing individuals that establish a founder population'.

Dispersal must also stand as a general background presumption in areas such as North Africa with its 'constant climatic disturbances . . . since the end of the Tertiary' (Quezel, 1978: 531); indeed, it is applicable to all areas of Africa during this present Quaternary phase of 'mobilism', to use Croizat's term. It can in fact be held (contrary to the views of Croizat's school) that the upheavals during Quaternary times show vicariance and dispersal events to be the two sides of the same coin (cf. Udvardy, 1981; Brundin, 1981). Vicariance and dispersal can be seen to accompany the contraction and expansion of ranges as they follow the cyclic changes in Quaternary climate. Expanding ranges at any one time show a radial pattern, a pattern of dispersal; while contemporaneously contracting ranges show relict patterns, characterized by fragmentation with incipient or actual vicariance. In the present post-glacial epoch, for example, groupings of ranges into radiating 'tropical' and contracting 'nontropical' faunas and floras are discernible in southern Africa (e.g. Poynton & Broadley, 1978): radiating patterns of a diversity of plants and animals seem centred on the warm eastern lowlands (Poynton, 1961), and they interdigitate with patterns showing fragmentation and sometimes taxonomic differentiation on isolated cool uplands (e.g. White, 1978; Poynton & Broadley, 1978; cf. Haffer, 1981, for South American birds).

There is a tendency in the vicariance vs dispersal debate, as presently conducted, to divert attention from the vicariant and dispersal events occurring all around us at the present time. At a symposium centred on vicariance held at the American Museum of Natural History in 1979 (Nelson & Rosen, 1981), Tattersall (1981: 410) remarked of Haffer's contribution on Neotropical bird speciation: 'Haffer's contribution seems likely to appeal more to those who view biogeography as a set of real-world problems seeking solution than to those who regard it as a science in search of a paradigm'. Yet, bearing in mind Popper's argument (Popper & Eccles, 1977: 39) that it is indeed 'real-world problems' that science starts from, it is hardly surprising if the current debate makes only limited sense to many of us studying patterns of current vicariance and dispersal in Africa. Does a vigorous science spend time 'in search of a paradigm'? The vicariance vs dispersal debate, as I have tried to show, has stressed the need for scientists to be philosophers also, and scrutinize the presuppositions and programmes within which they carry out their work. On that score we should avoid being faulted; yet beyond that, let us associate ourselves with the breadth and freedom of those like Wild and Levyns who, unconstrained by paradigms such as the anti-Wegenerism which gripped their overseas contemporaries in the 1960's, were ready to explore whatever Africa had to show them.

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The botanic garden in a changing world

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ABSTRACT

The paper deals with the development of the National Botanic Gardens of South Africa at Kirstenbosch in the Cape. This garden made history by concentrating exclusively on the flora of its own country. A series of regional gardens have also been established to display and cultivate local floras.

Internationally there has been a growing awareness of the necessity for conservation of natural resources. We have been in the forefront in conserving our vegetation, and in creating a 'gene' bank of indigenous plants.

Large numbers of species are introduced into our gardens, where they are cultivated, studied, displayed, and their place in the flora determined. But this is only the beginning.

Plants and vegetation must be evaluated within the total concept of the biological and physical milieu.

Research, into the taxonomy and cultivation of horticulturally promising taxa is undertaken and should be intensified. Botanic gardens are people-orientated and the information on nature available must be disseminated. The next stage in the development of our botanic gardens is the development of an education section.

The time has also come to consider the development of a parallel system of regional exotic botanic gardens to complement the present indigenous gardens. Such a development would be complementary to the original concept and not in competition. The South African flora will remain the most important subject in the N.B.G., but South Africans must also have the opportunity to learn about other floras.

RÉSUMÉ

LE JARDIN BOTANIQUE DANS UN MONDE CHANGEANT

Ce document traite du développement des Jardins botaniques nationaux à Kirstenbosch dans la province du Cap. Ce jardin est connu pour s'être concentré exclusivement sur la flore de son propre pays. Une série de jardins régionaux ont aussi été établis pour exposer et cultiver les flores locales.

A l'échelon international une prise de conscience grandissante quant à la nécessité de protéger les ressources naturelles, s'est développée. Nous avons été à l'avant-garde en protégeant notre végétation et en créant une banque de 'gènes' des plantes indigènes.

Un grand nombre d'espèces sont introduites dans nos jardins, où elles sont cultivées, étudiées, exposées, et où leur place dans la flore est déterminée. Mais ceci n'st qu'un début.

Les plantes et la végétation doivent être évaluées dans le concept global d'un milieu biologique et physique.

La recherche dans la taxonomie et la culture de taxa horticoles prometteurs est enterprise et devrait être intensifiée. Les jardins botaniques sont orientés vers le public et les informations disponibles sur la nature doivent être diffusées. Le stade suivant dans le développement de nos jardins botaniques est le développement d'une section éducative.

Nous sommes aussi arrivés au moment d'envisager le développement d'un système parallèle de jardins botaniques régionaux exotiques pour compléter les jardins indigènes actuels. Un tel développement serait complémentaire au concept original et non en concurrence. La flore sud-africaine restera l'objet le plus important des Jardins botaniques nationaux; mais les Sud-Africains doivent aussi avoir l'occasion de connaître d'autres flores.

A botanic garden is a biological entity: plastic, vibrant, dynamic and alive. The layout, the form, the competition and, very important, the objectives and aims, change from time to time depending on needs, opportunities, developments in other fields and even on fashion.

A botanic garden that does not change becomes static, docile, stodgy and moribund. And today we are living in dramatic times of frequent change and development.

It is essential to keep up with modern trends in presentation, display, techniques and interpretation. At the same time, however, adequate restraint and dignity must be observed.

A great garden can, through inadequate or faulty management, run out of steam and stagnate. Injections of new thoughts, objectives and ideals must be made continuously or at least periodically to keep the organization vibrant and vigorous.

We can ask the question then: what are the main requirements of a well-organized botanic garden today? I would say that it is a scientific, educational and cultural institution for the cultivation, display, scientific study and preservation of plants and plant species.

Regional botanic gardens

One of the most recent developments and a very significant one at that has been concern about the continued existence of rare, endangered or threatened species, many of whose future existence is in peril and which are perhaps on the brink of extinction.

It is generally accepted that the most effective method of saving such species is to maintain and preserve the complete habitat in which they grow. This is obviously not always possible. The next best approach is to attempt to cultivate them in a safe area which has the same or nearly the same habitat or environmental conditions.

The establishment of regional botanic gardens in various ecological areas of South Africa has done

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much to provide a number of localities where rare species indigenous to such localities can be grown.

The gardens which comprise the National Botanic Gardens of South Africa are:

1. Kirstenbosch Botanic Garden, Cape. This is the headquarters.
2. Karoo Botanic Garden, Worcester, Cape.
3. Harold Porter Botanic Garden, Betty's Bay, Cape.
4. O.F.S. Botanic Garden, Bloemfontein, Orange Free State.
5. Drakensberg Botanic Garden, Harrismith, Orange Free State.
6. Natal Botanic Garden, Pietermaritzburg, Natal.
7. Lowveld Botanic Garden, Nelspruit, Transvaal.
8. Transvaal Botanic Garden, Roodepoort, Transvaal (Operations have not yet commenced.)

Although the general policy to display, cultivate, study and preserve the indigenous flora is more or less the same in each garden, the gardens themselves differ tremendously from one another as far as climate, soils and all other environmental factors are concerned. In Kirstenbosch, the mother garden, the aim is to establish as many as possible of the 18 000 native species of South Africa, but each of the regional gardens concentrates exclusively on the species which occur naturally in their respective areas.

I believe that it is true that Kirstenbosch has pioneered, on a world scale, the concept of developing regional botanic gardens throughout the country for the cultivation and conservation of the native flora. These ideas have been followed with interest by colleagues in many lands. At an International Conference which I attended at Kew in 1978 one of the main resolutions was that:

> 'This Conference agrees unanimously . . . and stresses . . . how essential it is that all countries, where applicable, should have a suitable network of national regional botanic gardens to fulfil their fundamental part in the management and conservation of natural resources'.

Kirstenbosch was specifically mentioned as the originator of this concept and as being the first institution to put it into practice.

Siting of garden

Although a botanic garden is neither merely a city pleasure park nor simply a nature reserve, it should be situated in as pleasing and beautiful a locality as can be found within easy distance of a city or large town as possible, thus making it easily accessible to a large number of people. As a botanic garden is a scientific and educational institution, it is desirable that it should be near universities and schools. An attractive natural setting or surround uncluttered by buildings or other man-made structures on the horizon is a decided advantage.

Its beautiful backdrop of rugged rocky buttresses on the eastern slopes of Table Mountain contributes in no small measure in giving Kirstenbosch the reputation of being perhaps the most beautiful botanic garden in the world. Mountain streams flow over cascades and waterfalls through naturally forested areas before entering the garden itself.

The garden which was founded in 1913 is 12 km from the heart of Cape Town and covers an area of 528 ha of which 60 ha are under cultivation. The altitudinal range is from 100 m to over 1 000 m above sea level.

When establishing a new garden it is most desirable to select a site with uneven topography, water features, interesting natural vegetation and an unbroken skyline. It is fortunate that we have been able to achieve this in Kirstenbosch and in its regional gardens. As can be expected, the Karoo Botanic Garden does not have any water features.

As far as possible, buildings are kept away from the central parts of the gardens and are located on the perimeter so as not to intrude into the garden areas. A programme for the building of a large new head office complex on the edge of the garden is soon to be commenced at Kirstenbosch. This will include administrative offices, herbarium, information centre, laboratories, store rooms and an auditorium. These will largely replace buildings which are at present in the garden and which will be completely removed.

Layout

Careful planning provides a layout which is both artistically attractive and scientifically functional. A botanic garden is frequented by people who seek knowledge and beauty and it is important that the display and presentation of the plants achieve this object. The basic principles of the layout can be taxonomic, morphological, ecological or geographical.

Research

A collection of gardens representing as far as possible the various ecosystems in a country is invaluable for research on plants and their relationships, not only between plant species, but between vegetation and environment and the dependence of plant on insect and animal, and of animal and insect on plant. In other words, plants and vegetation must be evaluated within the total concept of their biological and physical milieu.

G. J. Broekhuizen has conducted research on the biological relationships of the Orange-breasted Sunbird *Anthobaphes violacea* and the Cape Sugarbird *Promerops cafer* in the fynbos at Kirstenbosch and Wiens and Rourke have worked on the pollination role of rodents on some species of *Protea.*

Research is a fundamental requirement of an efficiently organized botanic garden and a herbarium is an essential part of it. The herbarium furnishes the scientific nucleus for the gardens without which the gardens could not rightly claim the title 'Botanic'; in fact, it can be said that the herbarium is the pulsating heart of the whole institution.

In 1956 the South African Museum in Cape Town transferred its herbarium, the oldest in the country, to Kirstenbosch on permanent loan to be amalgamated with the Compton Herbarium. The total number of mounted sheets in the Compton Herbarium is now about a quarter of a million.

Each of the regional botanic gardens has its own herbarium, concentrating on the flora of the region which it represents. The first sets of all the regional gardens collections are filed in the Compton Herbarium.

Our research on the South African flora is centred in the Compton Herbarium and papers and monographs are produced from time to time. The volume of production is unfortunately lower than we would like. This is due in large measure to the present lack of space, funds and staff, a situation which I hope will be remedied when the new head office accommodation has been provided.

Taxonomic research, although very important, is certainly not the only type of research that should be carried out in a botanic garden. Many fields of investigation with a bearing on the activities of a botanic garden should be undertaken and are associated with ecology, physiology, pathology, cytology, genetics and with all aspects of horticultural science. For the reasons already given, not very much has been achieved in these fields at Kirstenbosch.

Education

A botanic garden plays a very important role in providing information to university students, school children and members of the general public. The education role may be direct and specific or it can be more indirect and subtle.

The Director of the gardens is one of the Professors of Botany at the University of Cape Town, thus maintaining the link that was formed when Harold Pearson, Professor of Botany at the University founded the gardens in 1913 and became the first Director.

Two qualified school teachers give instruction in nature study every school day of the year to classes of school children who come to the gardens for this purpose. Part of the instruction is given in the classrooms, but most of it takes place in the garden.

Honorary guides and guide-lecturers are provided for members of clubs, societies and other organized groups.

Most activities in a botanic garden are associated in some way or other with education. For example, the adequate labelling of plants has an educational function: it is telling the visitor something about the plant he is viewing. This is all part of the interpretive services rendered by a garden.

To meet the strong public demand for information, a well-balanced education programme should be maintained with the necessary staff and facilities to make it worthwhile both nationally and internationally. The education/information service should take on many forms, e.g. the plant collections should be provided with brief explanatory notices, self-guided tours and brochures, slide shows with synchronized tape commentaries, guided walks, short courses ranging from horticulture to demonstrations and programmes to involve visitors in some worthwhile project, etc.

Conservation

Much has been written about earlier times when persons were sent to collect plants from the furthest ends of the earth for botanic gardens, for growing or for scientific study. Sir Joseph Banks in England was responsible towards the end of the eighteenth century for sending collectors to all parts of the world to get plants for Kew Gardens. Wilfred Blunt in his 'In for a Penny' (1978) tells of Banks who was 'one of those who feel the irresistible urge to go to some remote, improbable, uncomfortable part of the world from where, unless they succumb to the climate or the assegai of an unsympathetic native, they ultimately return with a cornucopia of plants, seeds and herbarium specimens . . . two hundred years ago there was almost everything still to be discovered.'

Today the emphasis has changed completely to the collection of local species. One of the encouraging facets of international thought in recent years has been a growing awareness of the absolute necessity for conservation of all natural resources. The National Botanic Gardens of South Africa has been in the forefront in stressing the importance of the preservation of our vegetation, on which all other life depends, and in the creation of a gene bank for all indigenous plants.

Plant collecting

It is the function of all botanic gardens to collect plants for growing in the garden and for study in the herbarium. Our accent is largely on species that are rare or threatened. Thus every known species of *Encephalartos,* several of which are very rare, is in our collection. Others can be mentioned, for example *Serruria florida, Protea aristata, Orothamnus zeyheri, Moraea loubseri, Erica fairii, Brunia stokoei* and many succulents, including *Pachypodium namaquanum.*

The endangered plant study group of the University of Cape Town has made a list of species which are threatened or endangered in the Western Cape. Of these we are successfully growing and cultivating no less than 280 at Kirstenbosch.

Distribution

Throughout the world, every botanic garden worthy of the name publishes an Index Seminum of seeds available for free exchange to botanic gardens or other scientific institutions. At Kirstenbosch another list is published and sent to each of the almost 8 000 members of the Botanical Society of South Africa who are entitled to a quota of seeds free of charge, the quota ranging from 15 to 20 packets annually, according to class of membership.

Free seed despatched to botanic gardens and to members of the Botanical Society since 1953 increased from 16 064 packets to 40 890 packets in 1974 and to 50 092 in 1981.

The distribution of seed by botanic gardens is a usual practice, but this cannot be said about the distribution of flowering material. The National Botanic Gardens of South Africa is an exception. At many international congresses or exhibitions wild flowers from Kirstenbosch are despatched to provide decorative displays and named exhibits. The main objectives in doing so are to stimulate an interest in our unique flora and also to promote international goodwill. During 1981 no less than 3 640 kg of cut flowers were sent to destinations such as the United Kingdom, Spain, Austria, West Germany, Australia, Italy, France, Japan, Hong Kong, Taiwan, Greece and Switzerland.

Recording

The keeping of proper records is a function of any scientifically managed organization. Index cards with adequate information which must be kept up to date are maintained for all collections in the gardens. They list data on source of the material, whether seeds, cuttings or whole plants with details of date, locality, description of the species in its natural environment, altitude, soil, climate type of vegetation community and so on. After the material has been obtained, the records indicate percentage germination, percentage survival, rate of growth, age and time of flowering, where planted out in the garden, any special treatment given and generally how the material responds to cultivation. In this way a total history is obtained of each plant.

Job satisfaction

The success of a garden depends very largely on the people who work in it. If they feel that they are important components of the whole institution and if they can have some share in decision-making they are likely to give loyal and dedicated service. Recently, staff members of Kirstenbosch and its associated gardens underwent an intensive course in management and organizational development organized for us by the School of Business Management of the University of Stellenbosch.

Botanical Society of South Africa

A botanic garden should not operate in isolation. It is important that in addition to its research role there should be public involvement and public participation in the activities of the garden. An organization of the 'Friends of the Botanic Garden' type is extremely useful in achieving this. It operates as the public arm of the institution and it can do much to assist in the important task of raising funds.

The Botanical Society of South Africa came into existence at the same time as the National Botanic Gardens of South Africa mainly to support the young enterprise in all its activities. The relationship between gardens and society is a very close one and the members feel that they have a participating share in the welfare of the gardens. The society has a finger on the pulse of modern developments and is able to assist the gardens to keep pace with advances in a changing world.

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Plants Africa gave to the World

G. KUNKEL*

ABSTRACT

Although the flora of Africa is rather poor in plant species when compared to the floras of Tropical America or South-east Asia, this vast continent is the home of a wide range of plants useful to Man. Many of these have become famous in cultivation around the world. Coffee now provides an important source of income for certain countries, and the Yams yield one of the world's staple foods. The Oil Palm and Cola trees are widely cultivated in Africa itself and elsewhere. African Mahoganies and Ironwoods are much sought after timber trees of excellent quality. Numerous grasses and pulses are well-known for their food value, and some of the native Cucurbitaceae are appreciated additions to our vegetable diet.

African plants have also made their contribution to horticulture, ranging from world-famous trees such as the African or Gabon Tulip tree and many of the South African species of Proteaceae to the multitude of East and South African succulents.

The present paper provides a survey of the most important of these useful plants and will emphasize the need of further research for forestry and agricultural as well as horticultural purposes, especially as far as some still little-known but potentially important plants species are concerned.

RÉSUMÉ

LES PLANTES QUE L'AFRIQUE A DONNÉES AU MONDE

Bien que la flore d'Afrique soit plutôt pauvre en espèces végétales quand on la compare aux flores de l'Amérique tropicale ou du Sud-Est asiatique, ce vaste continent est le berceau d'une large gamme de plantes utiles à l'homme. Beaucoup de ces plantes sont devenues renommées dans les cultures pratiquées partout dans le monde. Le café procure maintenant une importante source de revenus pour certains pays et les ignames sont une des principales sources d'alimentation du monde. Le palmier à huile et les colatiers sont largement cultivés en Afrique aussi bien qu'ailleurs. Les acajous et bois de fer africains sont très recherchés pour leur bois d'excellente qualité. De nombreuses graminées et légumineuses sont bien connues pour leur valeur alimentaire et certaines cucurbitacées sont des suppléments appréciés de notre alimentation en légumes.

Les plantes africaines ont aussi apporté leur contribution à l'horticulture, allant des arbres mondialement renommé tel que le tulipier africain ou du Gabon et beaucoup d'espèces sud-africaines de Protéacées jusqu'à la multitude des plantes succulentes de l'Afrique l'Est et du Sud.

Le présent document fournit un relevé des plus importantes de ces plantes utiles et souligne le besoin de recherches plus poussées dans les domaines forestiers, agricoles et horticulturaux, spécialement pour les espèces végétales encore peu connues mais potentiellement importantes.

INTRODUCTION

As some investigators see it, and as we may well accept: Africa is a mother. Islands and continents have separated from her, have floated or broken away, thereafter to become independent in every sense and free to develop their own nature, usually more richly and with more diversity than before. And, whereas nature and her components in these segregated parts of the world have become adventurous in number, form, colour and expression, the world of Africa — 'mother's world' — has remained almost stagnant, static, and willing to give up her last secrets. We cannot really blame 'Mother Africa' for being poor both in number and diversity: especially, as the continuous deterioration of climatic conditions on the one hand and the influence of man's greed and ignorance as colonizer and user of the land on the other have left the all too familiar exploited landscapes so difficult to convert again into useful or restful countrysides. In other words, we have done almost everything possible to exploit this old continent leaving behind an exhausted land-mass and its biota which, ironically enough for the survivors, is now troubled by all and everything that Man could possibly think of.

However, mother-continent Africa has done more than to give birth to other land-masses, and more than to produce lions, elephants and giraffes. Africa is the home of some of the finest ornamental plants the world knows, and has given (and is still giving) her exploiters timber, shelter, and food. And, although this generosity, in general view, is scarcely appreciated, many of the species which farmers and gardeners have taken into cultivation are now favourites in extra-African gardens, or are important food-crops for many millions of people in tropical Asia and in America.

But Africa is a large continent and, although rather well explored, certain territories and certain taxonomic groups of plants (all critical enough) require our attention: the first to be better known and mapped and the latter to be cleared-up. Some of these aspects were mentioned at the last AETFAT-Meeting, in Las Palmas 1978 (Kunkel, 1979) but, more urgent still, much work remains to be done in the form of exhaustive studies on the uses of all indigenous plant species, the knowledge gained to be preserved for future needs before supermarkets and imported prejudice result in the loss of this valuable knowledge. I believe that our present level of knowledge concerning the use and application of African wild plants (which should not restrict itself to phanerogams, only) is still scratching at the

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*EDEZA, Carr. a Pechina, Viator, Almeria, Spain.

surface and has a long way to go before reaching the roots. Let us hope that we shall have the time and opportunity to do so.

The present paper should not be mistaken for an 'inventory' of all available material. It is offered as a contribution, and as a call for action. It is hoped that it will draw attention to facts already known, as well as to the potential of some lesser known plants and to others as yet quite unknown; here I prefer not to use the expression 'potential of underexploited material', an ugly term to be avoided.

SOME AFRICAN FOOD PLANTS

Beginning with what I consider to be Africa's economically most important plant species, *Elaeis guineensis,* I need hardly discuss it further. This is the West African Oil Palm, so essential for use by humans in nutrition and industry, but also providing palm-wine and so-called palm-cabbage, although the gathering of a 'cabbage' usually means the end of a particular specimen. *Elaeis* is now widely cultivated in South-east Asia and in tropical America (some authors even suggest that this species is of American origin!). Many new and improved cultivars and infraspecific hybrids have been developed outside the original range of the species, and probably a good many of them have not yet reached their ancestral homeland. Of other palms, the widely occurring Coconut Palm *(Cocos nucifera)* and the Date Palm *(Phoenix dactylifera)* are not considered as natives of Africa. However, certain species of *Raphia* are, and these have gained international repute as the source of the famous Raffia used in many forms of wicker-work, for weaving and in other handicraft. And there are species of *Hyphaene* and *Borassus,* both highly ornamental, and providing edible fruits and palm-cabbage; it is interesting to note that *Borassus* is also a source of sugar for local use.

Most food plants now grown in Africa are of extra-African origin: I refer here of course to the most important species, namely rice and mandioca (or cassava). There are, however, native millets (i.e. species of *Echinochloa, Eragrostis,* and a complex of *Pennisetum* with many synonyms), and sorghums (especially *Sorghum bicolor*), some of which have been taken into cultivation in other tropical countries.

Important providers of starch and food in general belong to the widespread and much cultivated genus *Dioscorea,* the yams or potatoyams, with several species native to Africa where they provide the basis of daily staple food; some of these species are also cultivated outside the continent of Africa.

Other important food plants from Africa such as the Abyssinian Pea (*Pisum* sp.), the Pigeon Pea *(Cajanus cajan),* the Bambarra Pea *(Voandzeia subterranea),* and other legumes like *Canavalia virosa, Psophocarpus* and *Vigna* spp. are cultivated here as well as in other regions of the world. Also of special interest are the African members of Cucurbitaceae of which some species *(Telfairia)* have seeds used for their oil-content, others (i.e. *Acanthosicyos, Momordica* and *Cucumis*) are used as vegetables. *Citrullus lanatus* (or *C.vulgaris?*) has become famous throughout the world, relished and known as the Watermelon. Some Cucurbitaceae still remain in need of investigation for their potential value (Jeffrey, 1979).

Together with the above-cited Oil Palm two other native oil-producing species of trees should be mentioned: *Butyrospermum parkii,* the Shee-butter Tree of the savanna countries north of the Equator, and (is it still called by this name?) *Tieghemella heckelii,* the Makoré or Edinam (or just the Butter Tree), a very tall species of the rainforest. Both genera belong to the Sapotaceae, and both provide oil and fat for cooking and for the manufacture of margarine, soap and candles. Unfortunately both species have apparently encountered difficulties with their cultivation in other continents; nevertheless, the export of Shee-butter products from Africa amounts to over 30 000 tons, annually. Some oil is also produced by native species of *Olea,* mainly in southern Africa, and from North-east Africa is the Nug *(Guizotia abyssinica),* also known as Niger Seed and cultivated in Africa and in parts of South America. And, even if *Sesamum indicum* is really of Asiatic origin, there are more than 20 African species in the genus, and several of them are harvested for their oily seeds (Brücher, 1977). Connected with oil-products and not to be forgotten is *Ricinus communis,* used for mechanical and medicinal purposes (as we well remember); the oil can also be used for cooking, and the plant itself (although it may become weedy) is frequently cultivated as an ornamental.

Food is also provided by *Plectranthus* (Labiatae), the Kaffir Potato, and by species of the Musaceae some of which are considered as natives of Africa. One thinks first of the genus *Musa* itself, and then of the Ensat *(Ensete ventricosum),* a widely cultivated species with an edible corm; this same Ensat is often found as an ornamental. The so-called African Breadfruit is a name somewhat confusingly applied to such extremely different plants as *Encephalartos* (an ornamental gymnosperm) and *Treculia,* which belongs to the Moraceae.

Besides starch and oil-producing plants, there is the group (mainly of trees) renowned for their fruits. But, whereas introduced plants such as *Citrus, Mangifera, Carica,* some *Musa* etc. are usually grown in larger plantations, the native fruit trees are mostly kept where they occur naturally, that is to say, they are treated as 'wild orchards'. One may mention here species of *Ficus* (Moraceae), and the refreshing fruits of *Maesobotrya barteri* (Euphorbiaceae); the nuts of *Ricinodendron rautanenii* (also Euphorbiaceae) are a local staple food, as are the fruits and seeds of many other trees and shrubs, especially of the family Leguminosae. The fruits of *Mammea africana* are eaten but have never reached the fame and wide distribution of those of its American counterpart, *Mammea americana.* On the other hand, *Blighia sapida* (known as the Akee) became properly Americanized as a result of the slave trade.

Harpephyllum caffrum (Anacardiaceae), the Kaffir Plum, has entered cultivation. And there is the typical fruit-family, the Chrysobalanaceae. All African species of *Chrysobalanus* known as wild fruit trees have been united with *C.icaco,* by White (1976) and, if accepted, all these different forms should be called Icaco Plum, or Coco Plum. On the other hand, the genus *Parinari* of the same family and also appreciated for its fruits, has been segregated (again: if accepted) into three different genera. The classical Icaco Plum, however, is regarded as a true American species!

Other useful genera belong to the Malvaceae, and here we have species of *Abelmoschus, Gossypium* and *Hibiscus* all of which are grown as ornamentals, for their fibre, and as food-providers. Even some *Acacia* species count as food plants, as the gum of some of them is edible (Vassal, 1979). And there must be hundreds of other food-providers known to local people, but only very few of these plants are as yet known or used outside their home territory.

SPICES AND DRUGS OF AFRICAN ORIGIN

Africa has given the world several species of great economic importance as drugs, e.g. *Coffea.* This stimulant (main species cultivated: *Coffea arabica,* probably native in the Ethiopian region) has created wealth and employment in large areas of tropical America, and even South-east Asia has its own coffee-producing centres (Friis, 1979). Another stimulant of worldwide fame, as pointed out by Brenan (1979), has made its contribution in the form of species of the genus *Cola* (Sterculiaceae), especially *C.acuminata* and *C.nitida.* But there are at least five known species of the same genus (Brenan *l.c.*) of which the leaves are eaten as a vegetable.

Referring to spices, most peppers are of extra-African origin. However, two genera of two different plant families are native, being used locally (or misused as adulterants): species of the genus *Xylopia* (Annonaceae), an alternative for pepper, and a great number of species of *Aframomum* (Zingiberaceae), a substitute of the true Ginger. Several other genera provide substitutes for coffee or tea (i.e. *Catha edulis*), or are chewed as stimulants; most of these species (*Boscia, Cassia, Parkia* etc.) are of local importance, only, and none seems to be cultivated.

AFRICAN TIMBER TREES

Timber trees of Africa are legion. As everywhere in the tropics, there are soft- and hardwoods, white- and redwoods, yellow- and firewoods, ironwoods and other kinds of timber. Much of the world-famous Mahogany, supposed to originate in tropical America, for example, is supplied by African countries, needless to say being timber of somewhat different genera. However, the African substitutes for Mahogany are equally beautiful, and first-class timbers besides, and here one immediately thinks of the genera of the Meliaceae such as *Entandrophragma, Guarea, Khaya, Lovoa* and *Turraeanthus,* all of which yield an excellent 'mahogany'.

Other much sought-after timbers belong to different plant families, i.e. *Chlorophora* and *Antiaris* (Moraceae), *Lophira* (Ochnaceae), *Terminalia* (Combretaceae), *Heritiera* and *Triplochiton* (Sterculiaceae), *Mitragyna* and *Nauclea* (Rubiaceae), *Diospyros* (Ebenaceae), *Aucoumea, Canarium* and *Dacryodes* (Burseraceae), *Dalbergia* (Fabaceae), *Aningueria, Gambeya* and *Tieghemella* (Sapotaceae), and the large family of the Caesalpiniaceae, with genera such as *Afzelia, Berlinia, Distemonanthus, Gossweilerodendron, Guibourtia* and many others.

North Africa gave gardeners the famous Atlas Cedar *(Cedrus atlantica),* with its several cultivars; the South and East African Yellow-woods *(Podocarpus)* are much appreciated in carpentry, and *Widdringtonia* and *Tetraclinis* are other native Gymnosperms valued as timber and for reafforestation. East African species of *Juniperus* are called 'Pencil Cedar', and are used for this very purpose. A recent publication on African export timbers was presented by Dahms in 1979.

PLANTS WITH OTHER USES

Except for medicinal purposes, African trees with other uses are limited: since the cultivation of the American *Hevea brasiliensis* in Africa, the use of *Alstonia* and *Funtumia* (both of the Apocynaceae) and some lianas has vanished. *Ceiba pentandra* (an African species?) and several species of the related genus *Bombax* (and 'derivates') are still used locally for Kapok. But there are medicinal and rather important poisonous plants of international fame and reputation: genera like *Rauvolfia, Strophanthus* and *Strychnos* being the best known.

A tree with the most multiple uses (Wickens, 1979) seems to be *Adansonia digitata,* the Baobab; it provides timber and shelter, shade and fruits, water and medicine, fibre, food, tannin and various curious etceteras which includes the setting up of a prison in the great trunk of a Baobab.

AFRICAN ORNAMENTALS

If the section dealing with timbers is considered voluminous, this chapter on ornamental plants of African origin requires even more attention, because many famous plants of gardens and greenhouses, widely accepted and established all over the world, form a proud African 'family'.

It is difficult to give priority to any single species because most species have outstanding features, but as one usually thinks of trees first as 'superior beings', one may well open these remarks with trees; some ornamental palms and conifers have already been cited. Favourites of parks and larger gardens in the tropics and subtropics in general are the African Tulip Tree *(Spathodea campanulata),* the Sausage Tree *(Kigelia africana),* some Fig species (especially

Ficus afzelii and *F.lyrata*), species of *Erythrina (E.caffra, E.senegalensis),* of *Bauhinia* (i.e. *B. galpinii*), of *Dombeya,* of *Schotia* and others. *Carissa* and the related genus *Acokanthera,* from South Africa, are for example, frequent in most Canary Island gardens, and *Hibiscus schizopetalus* is not absent from any subtropical garden of distinction. Some species of *Acacia* are grown as shade trees and are very decorative in semi-arid landscapes; at least one of these, *Acacia karroo,* has become naturalized in some Mediterranean countries. *Cussonia, Millettia* and *Sparmannia* are greenhouse plants and of the kind prized by collectors.

World fame has been established for South Africa's Proteaceae, where genera like *Protea, Leucadendron* and *Leucospermum* have, together, some 250 species all of which are extremely 'garden-worthy'; cut flowers of *Leucadendron argenteum* (the Silver Tree) and *Protea cynaroides* (the King Protea) are first-class export articles to Europe and North America, although some of the material is now coming from horticultural establishments in Madeira. On the other hand, the equally numerous genus *Erica,* mainly of southern Africa, is relatively little known outside its natural habitats (Van der Spuy, 1971).

Widespread and popular garden plants of African origin are *Plumbago capensis* (now less aptly named *P. auriculata*), *Jasminum floribundum* (said to be native in the Nile region?), the 'Busy Lizzies' (*Impatiens oliveri* and *I.sultanii,* with their many cultivars), *Asparagus* species like *A.setaceus* (syn.: *A. plumosus*) and *A. sprengeri,* the Gazanias, the Gerberas, the Thunbergias, some beautiful Gardenias, and the highly varied and much cultivated complexes of *Streptocarpus* and the Saintpaulias or African Violets. *Tecomaria capensis* is well-known elsewhere, and so are some Labiatae like *Plectranthus, Pycnostachys* and, especially, the Lion's Ear or *Leonotis leonorus.* Much cultivated, but often running wild, is the Calla-lily *(Zantedeschia aethiopica),* and a truly weedy invader is the yellow-flowering *Oxalis pes-caprae,* Africa's only serious contribution to the list of world-infamous weeds.

Missing in this list, still, are *Ochna serrulata* (Ochnaceae), the mention of some Rubiaceae, especially the genera *Mussaenda, Randia* and *Pavetta,* the genus *Monodora* (Annonaceae), species of *Dorstenia* (Moraceae), the Breath-of-Heaven (*Diosma;* Rutaceae), the Cape Marigold (*Dimorphotheca,* a Compositae), the Evergreen Grapevine *(Rhoicissus capensis),* the 'Burning bush' *(Combretum microphyllum)* and many others. But special mention goes to that astonishing group of Pelargoniums so very much cultivated all over the world. This varied complex of beloved climbing or hanging, bushy or potted and always flowering 'geraniums' with their uncountable races, hybrids and cultivars, is probably Africa's most important contribution to horticulture.

In the Monocotyledones, the genera *Cyanotis* and *Palisota* (Commelinaceae) have become appreciated greenhouse plants; *Cyperus papyrus* seems to be of African origin; some ornamental *Dracaena* species are African, and so are, probably, most species of *Sansevieria.* Who will forget the 'Bird-of-Paradise' flowers of *Strelitzia,* and who does not appreciate Liliflorae of genera such as *Agapanthus, Babiana, Bulbine, Clivia, Chlorophytum, Crinum, Dierama, Drimiopsis, Freesia, Galtonia, Gladiolus, Gloriosa, Haemanthus, Hypoxis, Ixia, Kniphofia, Nerine, Watsonia* and others, so well-known in our gardens?

But, also related to the lilies, are various genera of succulents such as *Aloe, Gasteria* and *Haworthia,* and with this we approach African succulents in general. The Elephant Bush or Spekboom *(Portulacaria afra)* is often grown as a hedge; *Cissus quadrangularis* is present in most succulent collections, and not absent are species of Asclepiadaceae, especially of *Caralluma, Ceropegia, Huernia* and *Stapelia,* all of these with remarkable flowers which are large, colourful, and rather smelly.

To the family of Crassulaceae belong widely cultivated and much admired species of *Cotyledon* and *Crassula, Kalanchoe* and *Bryophyllum* (which I would prefer to keep separate), the remarkable *Rochea,* the numerous *Adromischus* and others. Succulent *Kleinia* are related to *Othonna euphorbioides* and to *Senecio johnstonii,* the 'giant' of the Kilimanjaro. And succulents too, in the wider sense of the term, are the Mesembryanthemaceae, with most of the roughly thousand or so of its species native in southern Africa. I prefer not to cite the 125 genera of Herre's (1973) book, except for the more common *Carpobrotus, Lampranthus* and *Drosanthemum* familiar in so many gardens, and the often weedy appearance of some species of *Mesembryanthemum* as well as *Aptenia cordifolia.* As for the many species of *Lithops* and related genera, the so-called 'living stones', which I cannot help but admire, I wish I had a living collection of these glorious little plants hardly noticeable in the wild and much sought-after in cultivation.

Little remains to be said here on succulents because so many and important books have already been written covering the theme. As curiosities in collections, one finds the swollen 'trunks' of species of *Adenia* (Passifloraceae) and of *Adenium,* the latter being an Apocynaceae. And we have this surprising multitude of succulent Euphorbias, the mainly Arabic-African counterparts of the American cacti, with all imaginable and unimaginable forms and expressions, apparently with the exception that none has yet become an epiphyte. Many species of this complex have been taken into cultivation, including tree-shaped ones such as *Euphorbia excelsa, E. candelabrum, E. tetragona, E. triangularis* and *E. grandidens,* all of which may reach 12–15 metres in height (Palmer & Pitman, 1972).

A last and famous and highly specialized African plant to be mentioned is not a succulent nor a tree nor a proper shrub: growing in South West Africa (Namibia), the *Welwitschia mirabilis* (or *W. bainesii,* as this very odd-looking gymnosperm is now called) must try amazingly hard to keep alive for about a hundred years, because it hardly ever rains in that region.

CONCLUDING REMARKS

As it appears both difficult and superfluous to make concluding remarks by summarizing a summarized report, I prefer to conclude with that which evidently remains to be done:

Africa is a palaeo-continent with limited resources, but with a great number of extremely interesting plants, plant-formations and entire landscapes each of which deserves more protection and planning than is given at the moment. Nature in Africa is also in need of thorough and supraregional investigations into the actual and the potential use and application of the known and the suspected 'useful' elements of its flora, for their nutritional, medicinal, industrial, ornamental and other properties, in order that we shall know them as such.

It is herewith suggested than an 'Ethnobotanical Commission' be set up to study the matter and — hopefully within the framework of AETFAT — will report on achievements or any results obtained, to encourage more and future investigations in what we may name a Regional Natural Heritage.

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Les organismes du Précambrien terminal du craton ouest africain

E. BOUREAU*

RÉSUMÉ

Le Précambrien terminal (Lipalien) du Craton occidental de l'Afrique, dans l'Adrar de Mauritanie a livré, notamment dans le Guelb er Richât, de nombreux organismes à structure archaïque, souvent très simple. Il s'agit de coccoïdes groupés souvent en sphéroïdes plus ou moins complexes suivant un schéma évolutif qui a pu être établi avec précision. La compréhension des formes fossiles du Précambrien résulte en grande partie d'une interprétation que l'on fait d'un 'point noir' contenu, comme de celle que l'on adopte pour les émissions de substance que ces formes produisent. Comparés aux espèces actuelles, les organismes du Précambrien rappellent les Bactéries coccoïdes et les Cyanophycées.

Ces microorganismes sont à l'origine d'oolithes nullement minérales car elles contiennent des glucides colorables par le réactif de Schiff après action de l'acide periodique. Ces formes généralement sphériques, sont classées parmi les Oncolithes.

Ces organismes sont également à l'origine de puissants récifs calcaires ou dolomitiques qui atteignent des épaisseurs considérables et qui contiennent des Stromatolites connus en de nombreux points du globe. Les Stromatolites sont des *Conophyton*, des *Collenia* . . . Elles sont sphériques, lamellaires ou columnaires. Ces formations récifales atteignent en Afrique une épaisseur de 3 000 m dans l'Adoudounien à *Collenia* de l'Anti-Atlas, de 600 m dans le Zemmour, de 150 m dans l'Adrar de Mauritanie, de 100 m dans la falaise du Hank au nord du Bassin de Taoudeni.

ABSTRACT

THE ORGANISMS OF THE TERMINAL PRECAMBRIAN OF THE WESTERN AFRICAN CRATON

The terminal Precambrian (Lipalien) of the western African Craton, in the Adrar of Mauritania, has provided, especially in the Guelb er Richât, many organisms with an archaic structure, often very simple. It concerns some coccoides, often grouped in more or less complex spheroides according to an evolutionary pattern that could be accurately established.. The understanding of fossil forms from the Precambrian is, to a great extent, the result of an interpretation made of an included 'black spot', which one adopted for the emissions of substance produced by these forms. Compared to the present species, the Precambrian organisms recall the coccoid Bacteria and the Cyanophyceae.

These microorganisms are oolithes in origin and are by no means mineral, since they contain stain-sensitive glucides with Schiff's reagent following the action of periodic acid. These forms, usually spherical, are classified amongst the Oncolithes.

These organisms are also responsible for the massive calcareous or dolomitic reefs reaching considerable thickness and containing some known stromatolites in many parts of the world. Stromatolites are Conophyton, Collenia *. . . They are spherical, lamellate or columnar. These reef formations of Africa reach a thickness of 3 000 m in the Adoudounian of* Collenia *of the Anti-Atlas, of 600 m in the Zemmour, of 150 m in the Adrar of Mauritania, of 100 m in the cliff of Hank in the north of the Taoudeni Basin.*

GÉNÉRALITÉS

De nombreux organismes peuplent abondamment plusieurs gisements extrèmement fossilifères du Sahara occidental dans de Précambrien terminal (= Précambrien supérieur; = Infracambrien; = Lipalien). L'un des plus important est celui du Guelb er Richât, dans l'Adrar de Mauritanie (Fig. 1).

Les fossiles qui y furent découverts se révèlent comparables et synchrones avec ceux de certains gisements du Riphéen III de Sibérie et même avec ceux des Bitter Springs d'Australie.

Les couches des Richât ont été classées C_2 et C_5 par Théodore Monod. Elles ont donné à Clauer, en 1973, par la méthode de datation du Rubidium-Strontium 964 ± 32 M.a. et 860 ± 35 M.a. Les fossiles étudiés proviennent des couches de C^{IIbis} datées −800 M.a. et qui précèdent largement la tillite de base du Cambrien à −600 M.a.

Pour comprendre les différentes formes des Richât de Mauritanie, on peut déterminer l'évolution probable à partir de certaines formes archaïques

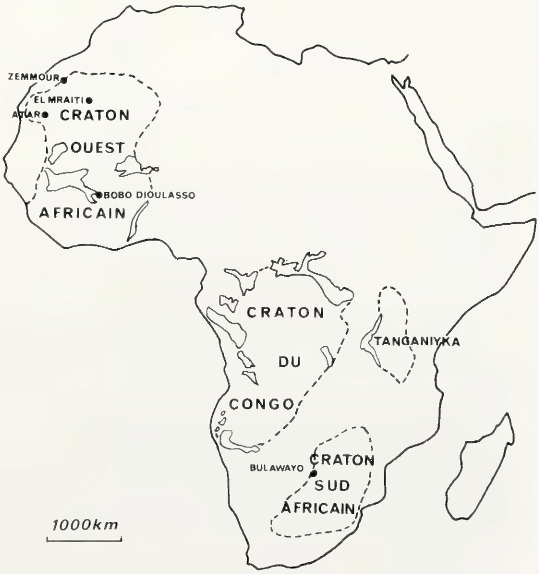

FIG. 1.—Répartition des divers Cratons au Précambrien en Afrique.

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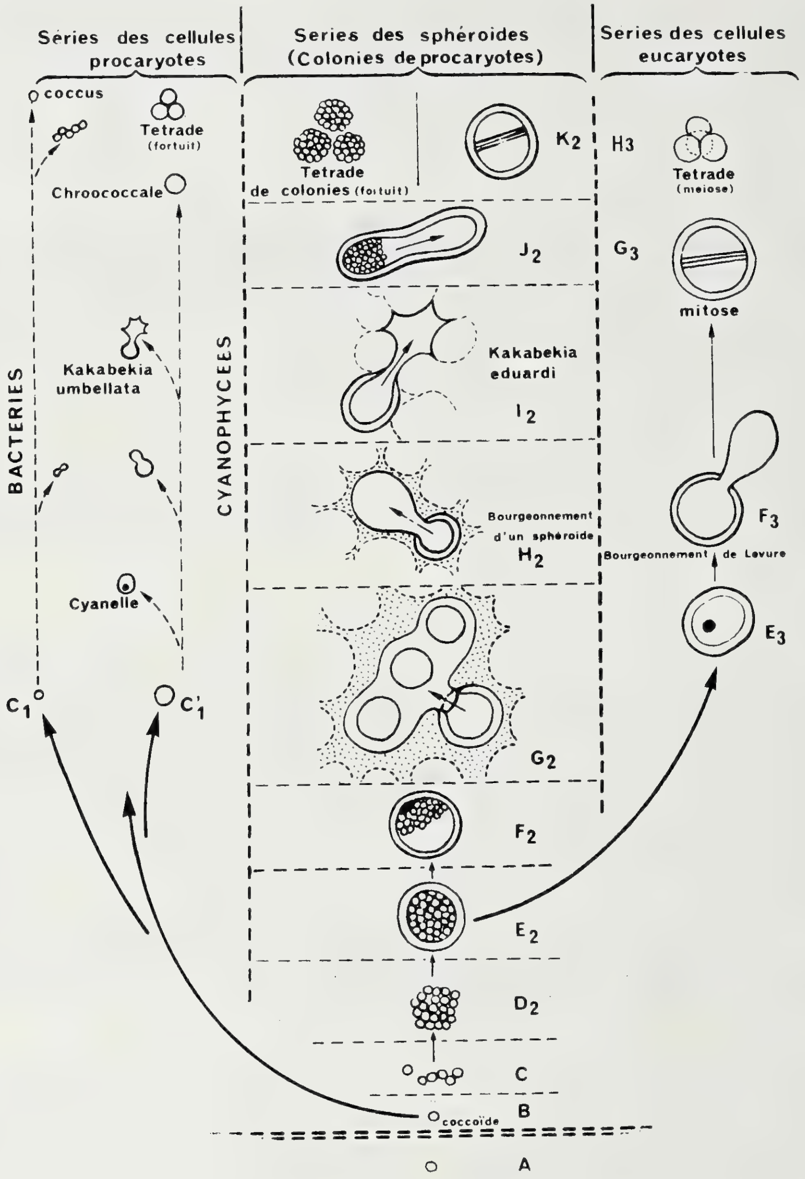

FIG. 2.—A, Sphérule issue d'un microcoacervat donnant naissance à un coccoïde vivant (B). **Série des cellules procaryotes.** C_1, Coccoïde isolé, souche d'une série d'organismes pouvant se diviser en conduisant aux Bactéries modernes: coccus . . . etc. C'_1, Coccoïde isolé, souche de la série des Cyanophycées, montrant parfois des formes dégradées (Cyanelles) à 'globule énigmatique' ayant l'aspect d'un pseudo-nucleus ('point noir'), pouvant être l'objet d'une division cellulaire ou donner naissance à un organisme ombelliforme *Kakabekia umbellata* Barghoorn) à la suite de l'écrasement d'une émission par les coccoïdes resserrés dans le voisinage. A cette série, appartiennent les Chroococcales, Cyanophycées unicellulaires, puis les formes filamenteuses. Les dispositions en tétrades sont fortuites: cf. *Nostocites vesiculosa* Maslov, 1929. **Série des sphéroides.** C_2, Les coccoïdes se divisent de façon répétitive et donnent des filaments. D_2, Des colonies massives en grappes se constituent rappelant *Sphaerocongregus.* E_2, Une paroi commune entoure la colonies de coccoïdes: cf. *Vesicularites saharianum* Boureau (1970). F_2, Les coccoïdes se localisent en un point précis de la paroi qui à ce niveau est lysée et donne un pore germinatif: cf. *Africano-spheroides fertilis* Boureau (1975). G_2, Par le pore germinatif une substance mucilagineuse est émise qui atteint un grand développement à la suite de l'adsorption des molécules situées dans un grand espace disponible. Plusieurs sphéroides peuvent s'y différenciés. H_2, l'espace disponible devenant limité l'émission est restreinte les substances adsorbées sont moins riches. Il s'agit d'une bourgeonnement simple (Fig. 4.2). I_2, Les sphéroïdes resserrés écrasent l'émission qui prend une forme en ombelle (*Kakabekia eduardii* Locquin, 1979) dont les côtés concaves epousent les marges convexes des sphéroides voisins. J_2, A la suite du pincement médian de la paroi d'un sphéroide, on observe une émission interne allant d'une moitié dans l'autre. K_2, dans un sphéroide du type E_2, on observe souvent un cloisonnement équatorial avec un 'phragmoplaste' qui se différencie en diaphragme-iris. = La disposition en tétrades des colonies, assez fréquente est fortuite. **Série des cellules eucaryotes.** E_3, La différenciation de certains coccoïdes, transformés les uns en noyau, d'autres en mitochondries, d'autres en chloroplastes, aboutit à créer une cellule eucaryote avec ses organites. F_3, Une cellule eucaryote de Levure émet un bourgeonnement simple comme en H_2. G_3, Au cours de la mitose, on retrouve les aspects de K_2. H_3, Le groupement en tétrades résulte d'une méiose.

dont les sphérules de 0,5 à 4 µm, à morphologie proche des coacervats, semblent bien à l'origine des coccoïdes du Précambrien. On pourrait objecter que les organismes du Précambrien terminal doivent différer notablement des premiers organismes du Précambrien inférieur, étant séparés d'eux par près de 3 milliards d'années. Or, on constate que de tels organismes éloignés dans le temps ont une morphologie très peu différente de celle des plus anciens qui soient connus. L'oxygène étant assez rare, l'évolution, de toute évidence, a été extrêmement lente.

Le développement de certains organismes précambriens a pu être défini suivant des modalités du tableau ci-contre (Fig. 2).

Pour déterminer des organismes du Précambrien, il faut tenir compte de leur diamètre, surtout de la nature chimique et la structure de la paroi et enfin, pour une bonne part de l'interprétation d'un 'point noir', organite souvent contenu à l'intérieur.

On a pu dans de nombreux cas, penser que certains des fossiles des Richât avaient une constitution purement minérale et qu'il s'agissait plutôt d'oolithes sans rapport avec une origine biologique quelconque. De fait, certains sphéroïdes ont perdu tout leur contenu qui aurait pu démontrer leur caractère vivant, mais dans de nombreux cas, il est possible de déceler dans leur paroi même, dans leur intérieur et à l'extérieur dans le mucilage émis, la présence de glucides à l'aide de la colorations spécifique obtenue avec la réaction de Schiff, après oxydation par l'acide periodique. Une coloration carmin très nette montre la présence évidente des polysaccharides.

D'ailleurs, le caractère vivant est dans certains cas, déjà clairement démontré par des interruptions caractéristiques de la paroi (Fig. 7.2).

Le 'point noir' a été l'objet de diverses appellations: 'minute granular body', 'black point', 'black body', 'black dot'.

L'interprétation qui en résulte est également très variable, et comme noyau ou pyrénoïde, dans les deux cas, elle indique une cellule eucaryote.

Or, cet organite peut être rapproché du 'corps énigmatique' (quelquefois double) signalé dans les Cyanelles (Lafargue & Duclaux, 1979)* ou des pseudonucleus observés dans des cellules de Cyanophycées dégradées 'post mortem' (Awramik, Golubic & Barghoorn, 1972).

Ainsi, le *Pilavia maculata* D. Z. Oehler, 1978 (diamètre moyen: 3,5µm) d'Australie qui était considéré comme difficile à déterminer (1 500 mA) contient un ou deux 'corps internes' de diamètre 0,5 à 0,9µm) et il s'agit non pas d'une cellule eucaryote mais presque surement d'une Chroococcale. Il en est de même du *Caryosphaeroides pristina* Schopf, et du *Glenobotrydion aenigmaticus* Schopf des Bitter Springs d'Australie (1968).

Tous ces amas internes surtout uniques au sein des organismes généralement sphériques et de tous diamètres sont constitués d'unités très petites qui lysent la paroi à la suite d'une production d'enzymes (Boureau, 1979) en un point précis permettant ainsi un bourgeonnement vers l'extérieur.

Ces observations peuvent parfaitement être étendues aux organismes des Richât, qu'il s'agisse de très petits coccoïdes, de colonies de forme irrégulière ou sphérique, ou encore de très grands organismes collectifs.

Il faut admettre en outre que dans leur évolution particulière à la fois longue et lente, les organismes précambriens ont pu conserver longtemps certains caractères archaïques des coacervats de départ sans atteindre le degré d'évolution assez avancé des formes actuelles placées en fin de phylum. Cela est très vraisemblable pour les Bactéries et les Cyanophycées, espèces procaryotes que l'on rencontre tout au long du Précambrien pendant une durée qui atteint près de 3 milliards d'années.

Les organismes des Richât de Mauritanie s'expliquent alors en fonction de ces dérivations. D'autre part, les échecs ont été très nombreux, car, rares sont les organismes qui sont parvenus au terme de leur développement. Il en résulte que les fossiles rencontrés dans le Précambrien représentent diverses étapes qui jalonnent toutes ces tentatives arrêtées plus ou moins tôt dans leur course vers la cellule eucaryote, objectif terminal très rarement atteint.

LES ORGANISMES SPHÉRIQUES DU PRÉCAMBRIEN DU CRATON D'AFRIQUE OCCIDENTALE

Mauritanie

On retrouve dans le Précambrien terminal de Mauritanie des formes déjà signalées dans d'autres gisements parfois éloignés dans l'espace et dans le temps. Il est fréquent de trouver des appellations différentes. Le Guelb er Richât de Mauritanie a livré:

1. *Metallogenium personatum* Perfil'yev (1962),
2. *Nostocites vesiculosus* Maslov (1929),
3. *Africanosphaeroides fertilis* Boureau (1975), Figs 2 F_2 & 3.4,
4. *Kakabekia umbellata* Barghoorn (1965), Fig. 2,
5. *Monodites princeps* Boureau (1977), Fig. 7.2,
6. *Asterosphaeroides monodii* Boureau (1976), Fig. 4.3,
7. *Asterosphaeroides richatensis* Boureau (1970),
8. *Babetosphaera africana* Boureau & Monod (1958), Fig. 4.2,
9. *Polysphaerula globulosa* Boureau (1975),
10. *Osagia mauritanensis* Boureau (1970),
11. *Vesicularites saharianum* Boureau (1970),
12. *Kakabekia eduardii* Locquin (1979), Fig. 2 I_2,
13. *Nubecularites* sp. Maslov (1937). Il s'agit probablement d'émissions de substances à partir d'un sphéroïde disparu pendant la fossilisation,
14. *Stellasphaeroides similaris* Boureau (1975).

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* Certaines références du texte, volontairement omises de la Bibliographie sommaire en raison de leur trop grand nombre, figurent dans les travaux signalés.

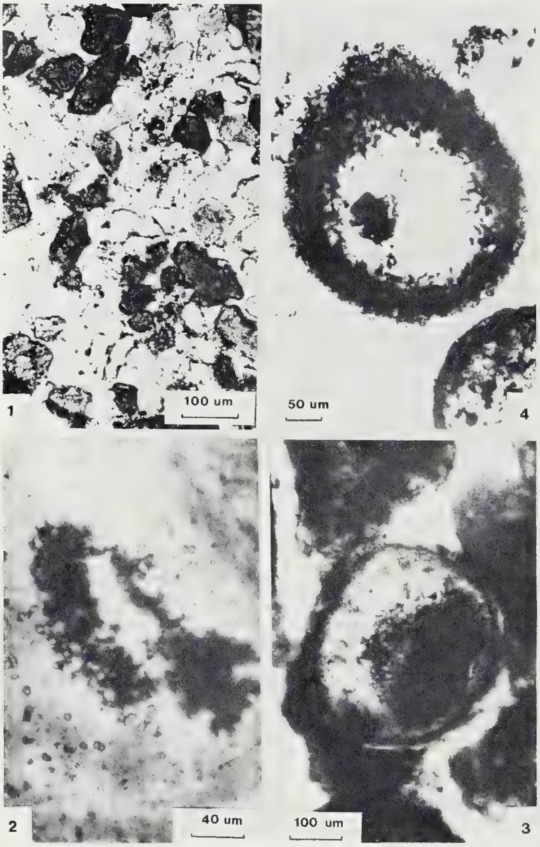

FIG. 3.—Précambrien terminal du Guelb er Richât de Mauritanie. Les parties noires de ces photographies indiquent la présence de glucides dans de lames minces entièrement colorées en carmin par le réactif de Schiff après action de l'acide periodique (sauf la photographie 4 préparée avant l'utilisation de ces réactifs). 1, Les amas sombres de forme irrégulière contiennent des coccoïdes avec leur mucilage très nettement coloré et une paroi commune en voie d'élaboration (comparable à E_2 de la Fig. 2. 2, Détail des coccoïdes partois isolés, en chainettes ou accompagné d'un mucilage abondant; 3, Les coccoïdes contenus dans un sphéroïde se sont concentrés en un point précis de la paroi commune qui subit à leur niveau, sous des influences enzymatiques, une lyse localisée avec production d'un pore (forme intermédiaire entre E_2 et F_2 de la Fig. 2. 4, *Africanosphaeroides fertilis* Boureau. Grand sphéroïde montrant de face un 'point noir' bien défini.

Certaines colonies ramifiées peuvent se rapprocher de formes décrites en URSS (Fig. 6):

Ramulostroma ramulosum Vologdin (1962),
Cyanostroma versiforme Vologdin (1962).

Africanosphaeroides fertilis Boureau, 1975 revêt une grande importance. L'espèce-type représente un sphéroïde de diamètre 400µm, avec un volumineux point noir de 80µm en rapport avec une concentration de micro-organismes internes visiblement responsables de l'ouverture de la paroi. Ce pore placé dans une petite dépression est lié à un cône d'émission placé sur les organismes dérivés.

La Fig. 2 D_2 rappelle le *Sphaerocongregus* Moorman (1973) de l'Alberta, Canada et Alaska (Allison & Moorman, 1973) qui montre des colonies dont le diamètre va de 5 µm à 16 µm et des cellules périphériques de 0,8 µm à 2 µm. Elles font également penser aux formes dites 'framboïdes' comme *Pyritosphaera barbaria* de 35 µm (Love, 1961) du Carbonifère d'Ecosse et retrouvées dans le Cambrien des Ardennes (Duchesne, 1963) ainsi qu'aux *Globulites* de 5 à 25 µm de Skripchenko (1968).

Mali

Les couches de Nara prospectées par René Dars au Mali ont un âge qui se rapproche de celui des couches des Richât. Le gisement lipalien de Korera a livré:

1. *Asterosphaeroides darsii* Boureau (1976),
2. *Osagia nersinica* Yakschin (1972).

De telles formes souvent associées se retrouvent au Sénégal (Dars, 1960).

Dans le synclinal de Taoudeni, en Afrique occidentale, l'âge précambrien supérieur des grès de Nara de Labbezanga semble appuyé par des fossiles signalés par Lopuchin (1971), jusque dans la tillite et notamment:

1. *Polyporama incrustata* Lopuchin (1971),
2. *Spumiosa spumosa* Naumova,
3. *Menneria roblotae* Lopuchin (1971).

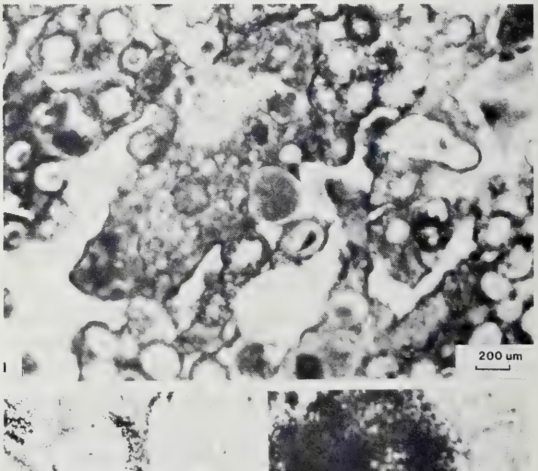

FIG. 4.—Précambrien terminal du Guelb er Richât de Mauritanie. 1, Issues de deux sphéroïdes, émissions de substance s'opposant dans un grand espace disponible (comparables à G_2 de la Fig. 2); 2, Sphéroïde *Babetosphaera africana* Boureau et Monod (1958) en voie de bourgeonnement (se reporter à la H_2 de la Fig. 2); 3, Organisme collectif en vue diamétrale (en bas); *Asterosphaeroides monodii* Boureau (1976) et en vue polaire (en haut), *Babetosphaera africana* Boureau et Monod (1958). Remarquer la disposition spiralée des filaments dressés sur un corps central et la paroi commune qui atteste le caractère vivant de l'ensemble.

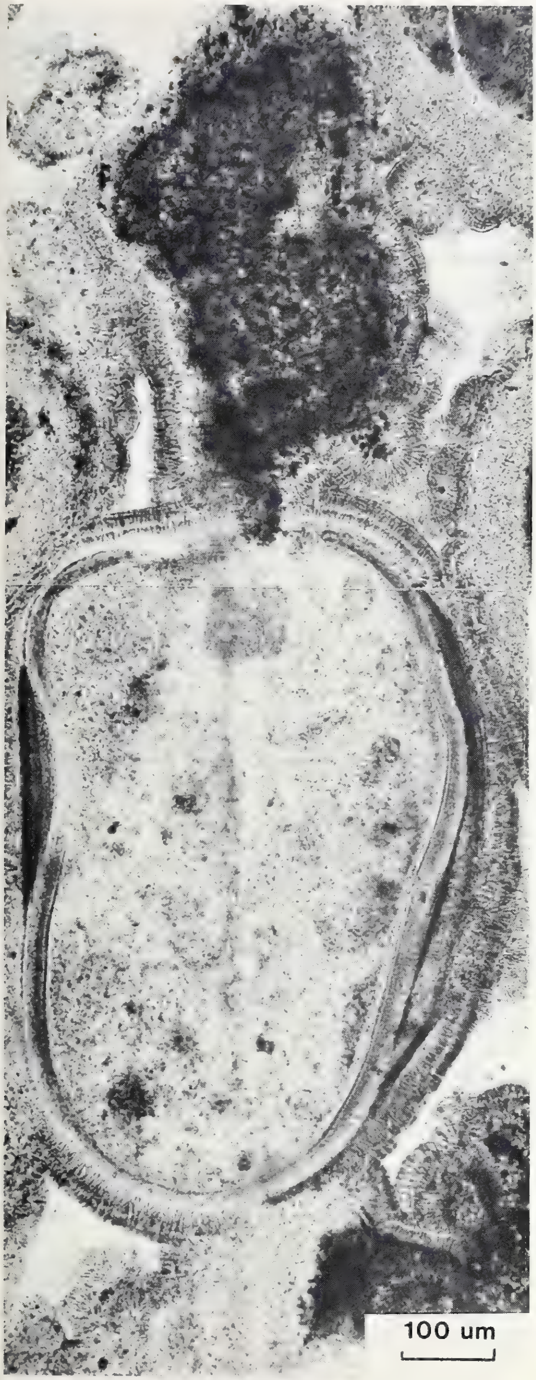

FIG. 5.—Précambrien des Richât de Mauritanie. Grand organisme à paroi lamellée, contenant des mocroorganismes, ouverte en un point permettant une émission externe de substance.

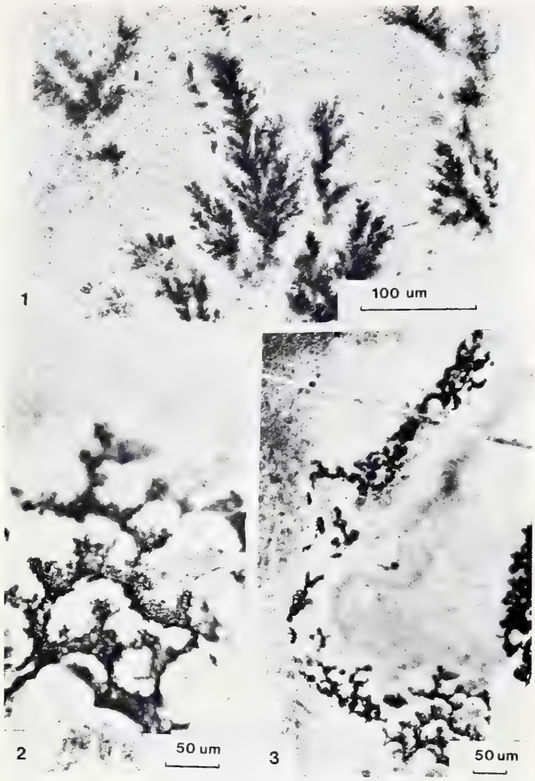

FIG. 6.—Précambrien terminal du Guelb er Richât de Mauritanie. Embranchement des Cyanophyta. Classe des Hormogoneae. Ordre des Sarmaellales. Famille des Plexostromataceae Vologdin (1962). 1, *Ramulostroma ramulosum* Vologdin (1962); 2 et 3, *Cyanostroma versiforme* Vologdin (1962). Colonies ramifiées-arquées sous deux grossissements.

Côte d'Ivoire

Une microflore a *Birrimarnoldia antiqua,* âgée de 2 milliards d'années a eté découverte en Côte d'Ivoire dans un sédiment birrimien de grauwackes et de pélites en rapport avec des formations volcaniques. Cette microflore décrite par R. Hovasse et R. Couture en 1961, contient des sphéroïdes de diamètre allant de 35 à 800 µm. Pour Hovasse, ces organismes pourraient être des Foraminifères alors que G. Deflandre y voyait avec raison sans doute, le résultat d'une activité bactérienne.

LES STROMATOLITES

On entend par stromatolites des structures organo-sédimentaires de dimensions inégales, allant du millimètre au décimètre qui s'accroissent à la suite de laminations créées par des sédiments fins sur des surfaces porteuses de microorganismes. L'activité métabolique de ces microorganismes producteurs de mucilages, joue un rôle de ciment pour les particules sédimentaires qui se trouvent ainsi piégées.

Les Stromatolites sont contenus dans de puissants récifs calcaires ou dolomitiques qui vont depuis le Sud marocain jusqu'en Afrique du Sud. Ils atteignent dans le Craton ouest-africain des épaisseurs considérables. Ils sont sphériques, lamellaires ou columnaires. Ces formations atteignent 3 000 mètres dans l'Adoudounien à *Collenia* de l'Anti-Atlas, de 600 mètres dans le Zemmour, de 150 mètres dans l'Adrar de Mauritanie, de 100 mètres dans la falaise du Hank au Nord du Bassin de Taoudeni, où la mer à stromatolites a été signalée pour la première fois par N. Menchikoff. C'est la

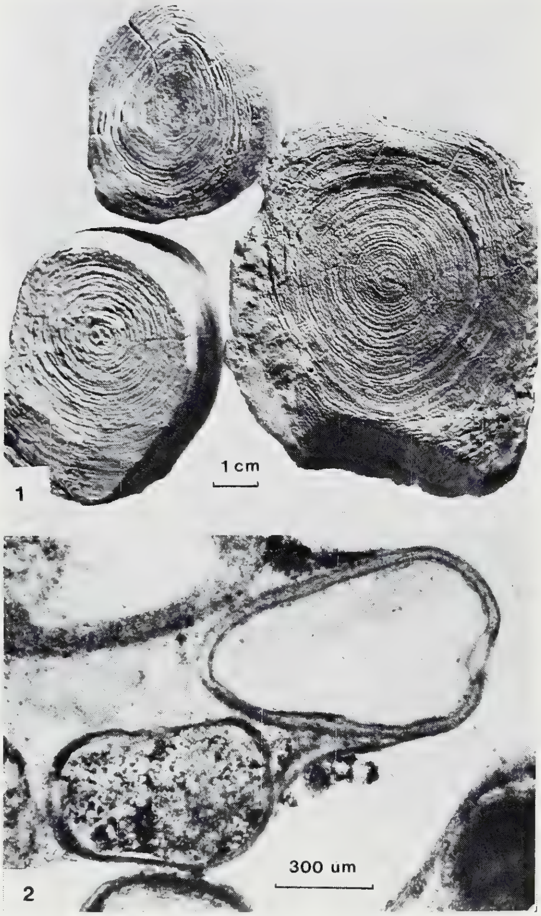

Fig. 7.—1, *Conophyton.* Stromatolites de l'Adrar de Mauritanie; 2, *Monodites princeps* Boureau (1977) montrant un pore unique. L'autre grand organisme placé au-dessous montre plusieurs ébauches de pores avec un contenu plus abondant en microorganismes.

série des Calcaires à stromatolites d'Atar avec les travaux de nombreux auteurs, F. Jacquet et Théodore Monod, ainsi que par Cl. Bense, René Dars, J. Delpy, J. Sougy, R. Trompette, M. Zimmermann.

En 1970, J. Bertrand-Sarfati et M. E. Raaben ont pu établir une étroite comparaison entre les Stromatolites de l'Oural et ceux du Sahara occidental. En 1972, J. Bertrand-Sarfati a fait une étude très complète des Stromatolites columnaires du Précambrien supérieur du Sahara Nord-occidental (Tableau 1). Janine Bertrand-Sarfati (1972) distingue 4 modes de laminations dans les Stromatolites columnaires:

1. Cas des *Conophyton ressoti* et *Baicalia mauritanica.*
Les microstructures en étui montrent une succession de minces feuilles de couleur sombre alternant avec des assises de calcite parfois traversées par des filaments d'Algues.

2. Cas de *Gymnosolen directus* et de *Tungussia nodosa.*
Les microstructures algales formant un tapis, sont souvent rassemblées en paquet et séparées par de grandes couches claires de calcite ou aragonite (sparite).

3. Cas de *Serizia radians* et de *Tungussia globosa.*
Les microstructures sont réparties en touffes.

4. Cas de *Tifounkeia globulosa* et de *Linella minuta.*
Des microstructures grumeleuses varient d'une colonne à l'autre ou dans une même colonne.

TABLEAU 1.—Craton ouest-africain: groupe des Stromatolites. (D'après J. Bertrand-Sarfati, 1972.)

Super-groupe	Groupe
Conophytonides	*Conophyton* Maslov
Kussiellides	*Jurusiana* Krylov
	Tarioufetia Bertrand-Sarfati
Tungussides	*Tungussia* Semikhatov
	Jacutophyton Schapovalova
	Baicalia Krylov
	Tilemsina Bertrand-Sarfati
	Parmites Raaben
	Kasaia Bertrand-Sarfati
	Serizia Bertrand-Sarfati
	Noutila Bertrand-Sarfati
	Tifounkeia Bertrand-Sarfati
	Linella Krylov
Gymnosolenides	*Gymnosolen* Steinmann
	Inseria Krylov

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Bothalia 14, 3 & 4: 479–480 (1983)

Index botaniques et études pastorales à l'IEMVT

J. P. LEBRUN* et A. L. STORK*

RÉSUMÉ

Les progrès réalisés à l'IEMVT, depuis la IXme Assemblée plénière de l'AETFAT, dans les projets suivants, traitant de la flore et des pâturages en Afrique, ont porté sur: 1, des index botaniques de cartes de répartition et d'illustrations de plantes (plantes vasculaires); 2, des études agrostologiques accompagnées de cartes des pâturages; 3, l'état actuel de l'herbarium et 4, une liste de publications botaniques de l'Institut depuis 1978. Un texte provisoire, ayant trait aux familles des Annonacées et des Euphorbiacées, a été rédigé pour un autre projet: 'Enumération des phanérogames d'Afrique tropicale'.

ABSTRACT

BOTANICAL INDEXES AND PASTORAL STUDIES AT THE IEMVT

Progress at the IEMVT, since the IX AETFAT Plenary Meeting, in the following projects dealing with flora and pastures in Africa, is reported on: 1, botanical indexes of distribution maps and of plant illustrations (vascular plants); 2, agrostological studies illustrated by maps of pastures; 3, the actual state of the herbarium and 4, a list of botanical publications of the Institute since 1978. In another project, 'Enumeration of the flowering plants of tropical Africa', a draft text dealing with the families Annonaceae to Euphorbiaceae has been written.

1. INDEX 1935–1976, DES CARTES DE RÉPARTITION DES PLANTES VASCULAIRES D'AFRIQUE

A la VIIIe réunion plénière de l'Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale (AETFAT), qui se déroula à Genève du 16 au 21 septembre 1974, nous avons proposé la rédaction d'un index des cartes de répartition des plantes vasculaires d'Afrique. Le 11 novembre 1977, c'était chose faite; cet outil de travail regroupait ± 12 800 références pour ± 8 800 espèces.

Actuellement un complément-supplément est réalisé et comprend aujourd'hui ± 7 550 références; la sortie de ce nouveau volume est effective depuis fin 1981.

2. INDEX ICONOGRAPHIQUE DES PLANTES VASCULAIRES D'AFRIQUE 1935–1980

Encouragé par le succès de l'ouvrage précédent, nous avons présenté à la IXe réunion plénière de l'AETFAT, (Las Palmas, mars 1978), un projet d'index des iconographies des plantes vasculaires d'Afrique, couvrant 45 ans de publication. Sa structure est identique à celle de l'index des cartes. Il regroupe ± 100 000 références; ce qui représente, en gros, le cinquième du nombre de références données par l'*index Londinensis,* dont la publication a malheureusement cessé en 1941.

Le Professeur Brenan, Directeur des Jardins Royaux de Kew, nous a fait l'honneur de rédiger la préface de notre ouvrage; sa publication est envisagée en 3–4 volumes. La sortie du premier d'entre eux est effective depuis fin 1981 (vol. 1, A–Cle, 27 500 références).

3. ETUDES AGROPASTORALES

Nous énumérons, ci-dessous, les principales études effectuées depuis le dernier congrès de l'AETFAT; nous regroupons sous ce qualificatif les travaux comportant des listes floristiques ou des cartes pouvant intéresser botanistes et phytosociologues, et les publications importantes.

AUDRU, J. & LAMARQUE, G., 1979. *Carte du ranch de la Marahoué au 1/20 000 (4 feuilles) avec légende explicative.* FED/SODEPRA/IEMVT.

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4. ETUDES BOTANIQUES

(a) *Herbier*

L'herbier de l'Institut d'Elevage (ALF) comprend au total ± 52 000 numéros dont ± 20 000 sont effectivement conservés à Maisons-Alfort en tant qu'herbier de référence réunissant plus de 4 800 espèces; le reste ayant été déposé au Muséum d'Histoire Naturelle de Paris, Laboratoire de Phanérogamie (P). De début 1978 à début 1981, environ 3 700 numéros ont été récoltés en Afrique nord tropicale.

L'ensemble des données liées aux récoltes botaniques est actuellement introduit en ordinateur; 30 000 d'entre elles sont déjà intégrées dans la base; la méthode utilisée est décrite en détails dans une publication spéciale (voir paragraphe suivant).

(b) *Publications*

Lebrun, J. P., 1977. *Eléments pour un atlas des plantes vasculaires de l'Afrique sèche* vol. 1, Etud. bot. 4, pp. 263.

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5. ENUMÉRATION DES PLANTES À FLEURS D'AFRIQUE TROPICALE

Lors du 'Business Meeting' de la IXe réunion plénière de l'AETFAT, nous nous sommes proposé de réaliser un tel travail. Un premier texte allant des Annonaceae aux Euphorbiaceae est actuellement écrit. Il doit maintenant faire l'objet d'une révision. A titre d'exemple, quelques pages ont été composées pour la présente réunion plénière et présentés à la faveur de la 'Poster session'.

Bothalia 14, 3 & 4: 481–495 (1983)

PRECIS, the Botanical Research Institute herbarium data bank

R. E. MAGILL*, G. E. GIBBS RUSSELL**, J. W. MORRIS† and P. GONSALVES**

ABSTRACT

PRECIS has been modified to make it more useful to taxonomists. The simplified system contains only specimen-related data, and the resulting decrease in the size of the data bank will make it more efficient to operate and maintain. The methods used to encode herbarium data, the operation of the storage and retrieval system, and several examples of system output, demonstrating the flexibility and versatility of PRECIS and its applications in herbarium curation and taxonomic research are described.

RÉSUMÉ

LE SYSTEME PRECIS, BANQUE DE DONNÉES DE L'HERBARIUM DE L'INSTITUT DE RECHERCHE BOTANIQUE.

Le systeme 'PRECIS' a été modifié pour le rendre plus commode à utiliser par les taxonomistes. Le système simplifié contient seulement des données relatives aux spécimens, et la réduction qui en résulte dans la dimension de la banque de données le rendra plus efficient à exploiter et à tenir à jour. Les méthodes utilisées pour l'encodage des données de l'herbarium, le fonctionnement de la mémorisation et le système d'extraction, ainsi que plusieurs exemples de sortie du système, démontrant la souplesse d'emploi du système 'PRECIS' et ses applications dans la gestion de l'herbarium et de la recherche taxonomique, sont décrits.

BACKGROUND

The computerized information system (PRECIS) developed for the National Herbarium of South Africa (PRE), as outlined by Morris & Glen (1978), became operational in 1980. Although the system functioned as it was designed, it became evident that its value to research at the Botanical Research Institute (BRI) was reduced by difficulties with maintenance and operation. After a trial period of approximately one year, the authors completely re-evaluated the system and provided a critical review of the system. The major difficulties with the system can be summarized as follows:

1. The system was too large (4 disk packs were necessary for on-line service) and the complex nature of the data base made programme maintenance and alterations difficult.

2. There was a large amount of extraneous information, and a high percentage of empty records (mostly information not available on older specimens) was carried by the system (Morris & Manders, 1981).

3. The high cost of routine inquiries of the data bank, the difficulty in manipulating and correcting the data and the slow turn-around of requests discouraged use of the system.

4. The specimen labels were in a cryptic format unsuitable for curatorial and research purposes.

In the light of these difficulties, the Botanical Research Institute decided to reassess the system according to Institute priorities, but with special emphasis on the specific requirements of herbarium curation and flora research. Datametrical Services reviewed possibilities for improved operation and efficiency of the system.

The problem of the size of the data bank and the extraneous information it carried (Morris & Glen, 1978) was the most serious. From the standpoint of herbarium curation and flora research, the system was overburdened with a great deal of peripheral, although related, information. This included information encoded under Economic Botany, Photography, Garden Records, and some broad ecological data (regional rainfall, degree of frost, soil depth and colour, etc.). The remaining taxonomic information was either specimen-related or species-related. Although there was an overlap of categories applicable to both groups, a further reduction in the size of the data bank could be brought about by the separation of specimen-related data and species-related data, where possible.

The problems of manipulating and correcting the data were traced to a single oversight in the encoding process (Morris, 1980): the computer number allocated to each individual specimen had not been recorded on the specimens when they were encoded. Because these computer numbers were not available, it was not possible to update the system in the most efficient and inexpensive way. The process of obtaining a listing of the computer numbers and attaching them to the specimens was tried, but was found too expensive in both computer time and man-hours. Another possibility, updating information only when data was extracted for research or curatorial purposes, was much too lengthy a process and would retard research in non-taxonomic areas, as well as hamper curation of the collection. Clearly, what the Institute needed, was quick, inexpensive

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access to the data on a specimen by specimen basis and by groups of related taxa.

The problem of cryptic specimen labels, was only partly correctable on the old system because of the way data was encoded. Although the format was adequate for data base operations, it was unsatisfactory for research and curation, especially to anyone unfamiliar with the system. It was clear that a method for producing complete and readable labels had to be designed.

Investigations showed that a simpler and more efficient system could be developed around a smaller data base with more clearly circumscribed requirements. Furthermore, it was found that the existing data base could be restructured for use in the new system.

THE NEW SYSTEM

Over a period of approximately one year, a new Herbarium Data System has been developed. The new system consists of three main parts. The first is a restructured version of the data bank for the 600 000 specimens at the National Herbarium, Pretoria (PRE). The second is a program (SPECUPDATE) that handles new data input, initial specimen output and permanent data file creation. The last part is the Burroughs-developed information retrieval system (INQUIRY).

1. *The data bank*

The data bank for the new system contains only specimen information. With the size problem of the old system in mind, the new system is restricted to data important to collectors, curators and taxonomic and floristic researchers. Although the system can be used to generate some species-related information from encoded specimen data (flowering times, substrate preference etc.), it has been accepted that a separate taxon-based data bank should be developed for this purpose. Thus, for instance, flower colour for the 890 specimens of *Acacia karroo* will not be stored for each specimen in the herbarium data bank, but rather only once under the taxon, in a separate species data bank, which will be developed in the future. This type of descriptive information can, however, be printed on the specimen labels (see below).

The data bank has been divided into 10 data sets, each containing 40–70 000 specimens (Tables 1 & 2). Specimen data for each of the four wings of the National Herbarium is contained in 2 or 3 data sets. Each set contains an exclusive range of taxon numbers referred to as genspec numbers (Morris & Glen, 1978).

TABLE 2.—Total number of taxa and specimens in each herbarium wing in PRE

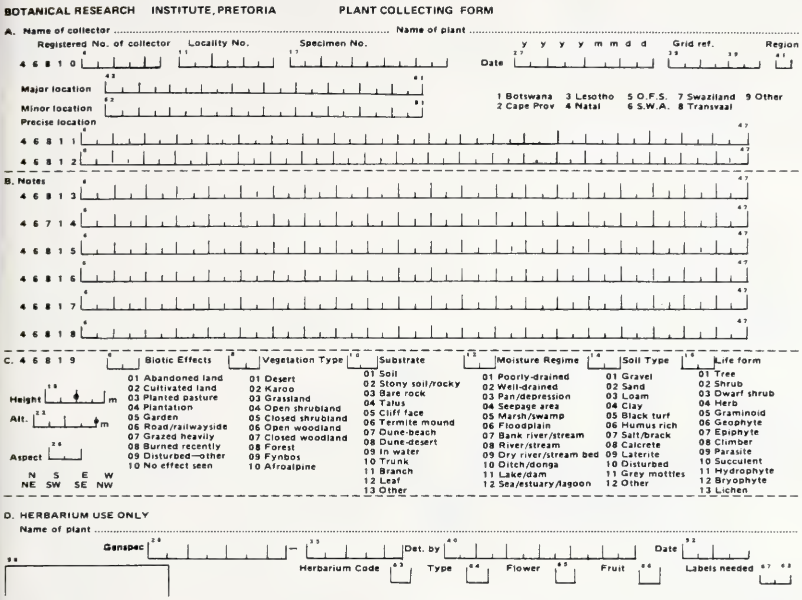
Wing	Genera	Species	Specimens
A	876	6 320	134 083
B	476	7 880	107 737
C	480	5 110	116 260
D	570	5 402	134 962
Total	2 402	24 712	493 042

As indicated above, the amount of data encoded for PRECIS has been reduced to make the information more manageable and accessible. Specimen data is now entered on collecting forms that give the collector more flexibility in recording data for the specimen lables and the data bank. The collecting forms (Fig. 1) are A5 in size and encoding is done on one side of the form only. The form is divided into four parts (A–D).

1.1 Part A contains collector and locality information (registered number of collector, locality number, specimen number, date, grid reference, region and major, minor and precise localities) that will appear on both the specimen label and in the data bank. It is possible to repeat this information for all specimens collected at a site by repeating only the collectors number and the locality number on subsequent collecting forms.

TABLE 1.—Data sets in PRECIS, with the taxa and numbers of specimens in each

Wing	File name	Families included	Genspecs	No. genera	No. species	No. specimens
A	CRYMON	Cryptogams – Eriocaulaceae (minus Poaceae)	0–832A	451	2 091	39 648
A	GRASSE	Poaceae	9900–9904	209	1 104	49 800
A	PETMON	Commelinaceae – Orchidaceae	896–1837	216	3 125	44 635
B	CASOXA	Casuarinaceae – Oxalidaceae (minus Fabaceae)	1855–3937	341	6 005	64 282
B	LEGUME	Fabaceae	3443–3910C	135	1 875	43 455
C	LINSTE	Linaceae – Sterculiaceae	3945–5091	196	2 139	59 915
C	OCHASC	Ochnaceae – Asclepiadaceae	5112–6924	284	2 971	56 345
D	CONSCR	Convolvulaceae – Scrophulariaceae	6968–7645	173	1 508	43 391
D	BIGOOD	Bignoniaceae – Goodeniaceae	7705–8716	171	1 377	32 270
D	COMPOS	Asteraceae	8734–9605A	226	2 517	59 301



BOTANICAL RESEARCH INSTITUTE, PRETORIA **PLANT COLLECTING FORM**

A. Name of collector .... Name of plant ....

Registered No. of collector Locality No. Specimen No. y y y y m m d d Grid ref. Region

4 6 8 1 0 Date

Major location

Minor location

1 Botswana 3 Lesotho 5 O.F.S. 7 Swaziland 9 Other
2 Cape Prov 4 Natal 6 S.W.A. 8 Transvaal

Precise location

4 6 8 1 1

4 6 8 1 2

B. Notes

4 6 8 1 3

4 6 7 1 4

4 6 8 1 5

4 6 8 1 6

4 6 8 1 7

4 6 8 1 8

C. 4 6 8 1 9

Height m

Alt. m

Aspect

N S E W
NE SW SE NW

Biotic Effects	Vegetation Type	Substrate	Moisture Regime	Soil Type	Life form
01 Abandoned land	01 Desert	01 Soil	01 Poorly-drained	01 Gravel	01 Tree
02 Cultivated land	02 Karoo	02 Stony soil/rocky	02 Well-drained	02 Sand	02 Shrub
03 Planted pasture	03 Grassland	03 Bare rock	03 Pan/depression	03 Loam	03 Dwarf shrub
04 Plantation	04 Open shrubland	04 Talus	04 Seepage area	04 Clay	04 Herb
05 Garden	05 Closed shrubland	05 Cliff face	05 Marsh/swamp	05 Black turf	05 Graminoid
06 Road/railwayside	06 Open woodland	06 Termite mound	06 Floodplain	06 Humus rich	06 Geophyte
07 Grazed heavily	07 Closed woodland	07 Dune-beach	07 Bank river/stream	07 Salt/brack	07 Epiphyte
08 Burned recently	08 Forest	08 Dune-desert	08 River/stream	08 Calcrete	08 Climber
09 Disturbed—other	09 Fynbos	09 In water	09 Dry river/stream bed	09 Laterite	09 Parasite
10 No effect seen	10 Afroalpine	10 Trunk	10 Ditch/donga	10 Disturbed	10 Succulent
		11 Branch	11 Lake/dam	11 Grey mottles	11 Hydrophyte
		12 Leaf	12 Sea/estuary/lagoon	12 Other	12 Bryophyte
		13 Other			13 Lichen

D. HERBARIUM USE ONLY

Name of plant ....

Genspec — Det. by Date

Herbarium Code Type Flower Fruit Labels needed

FIG. 1.—Plant collecting form.

1.2 Part B provides space for the description of the plant or other notes. This information can be in the form and style chosen by the collector and will appear on the specimen labels exactly as it was recorded. The data from part B is label information only and is not stored in the data bank.

1.3 Part C provides space for recording altitude, aspect and height of plants, and each will appear in the data bank and on the specimen label. A second group of blocks is provided to encode descriptive and environmental notes for the data bank only. Each subject field (biotic effects, vegetation type, substrate, moisture regime, soil type and life form) has its own descriptive terms listed on the encoding form. These fields should provide an abstract of the information given in part B, and do not appear on the specimen labels. This form of data storage is used because it is economical of space while providing a qualitative method for returning specimen data.

Part D is intended for use by the identifier of the specimen and contains space for the specimen's name, genspec number, determiner and date, computer number, southern African Herbarium code, type status, presence of flowers and fruit, and number of labels needed. The first four fields occur on the labels and in the data bank, the remainder appear in the data bank only.

2. *Specupdate*

This program is the heart of the new system. It is responsible for a large variety of functions including new data input, data set manipulation and maintenance, and initial specimen output in the form of encoded data and specimen labels. A brief review of the routine operation of this program follows: 1, as the collecting forms are completed they are grouped in bundles and encoded into data files; 2, data for each specimen is checked by the program for errors in each of the defined fields, and if none are found it proceeds to print all of the encoded information (Fig. 2); 3, this printout is returned to the collector or herbarium for approval or correction; 4, when approved, the program then prints the required number of specimen labels (Fig. 3), and simultaneously transfers the data into the proper wing data set. When this is completed the program removes the bundle from the data file.

The system also has several smaller programs designed to correct or update the information already stored in the wing data sets. These alterations can be made for individual specimens or in groups of related specimens.

3. *Inquiry*

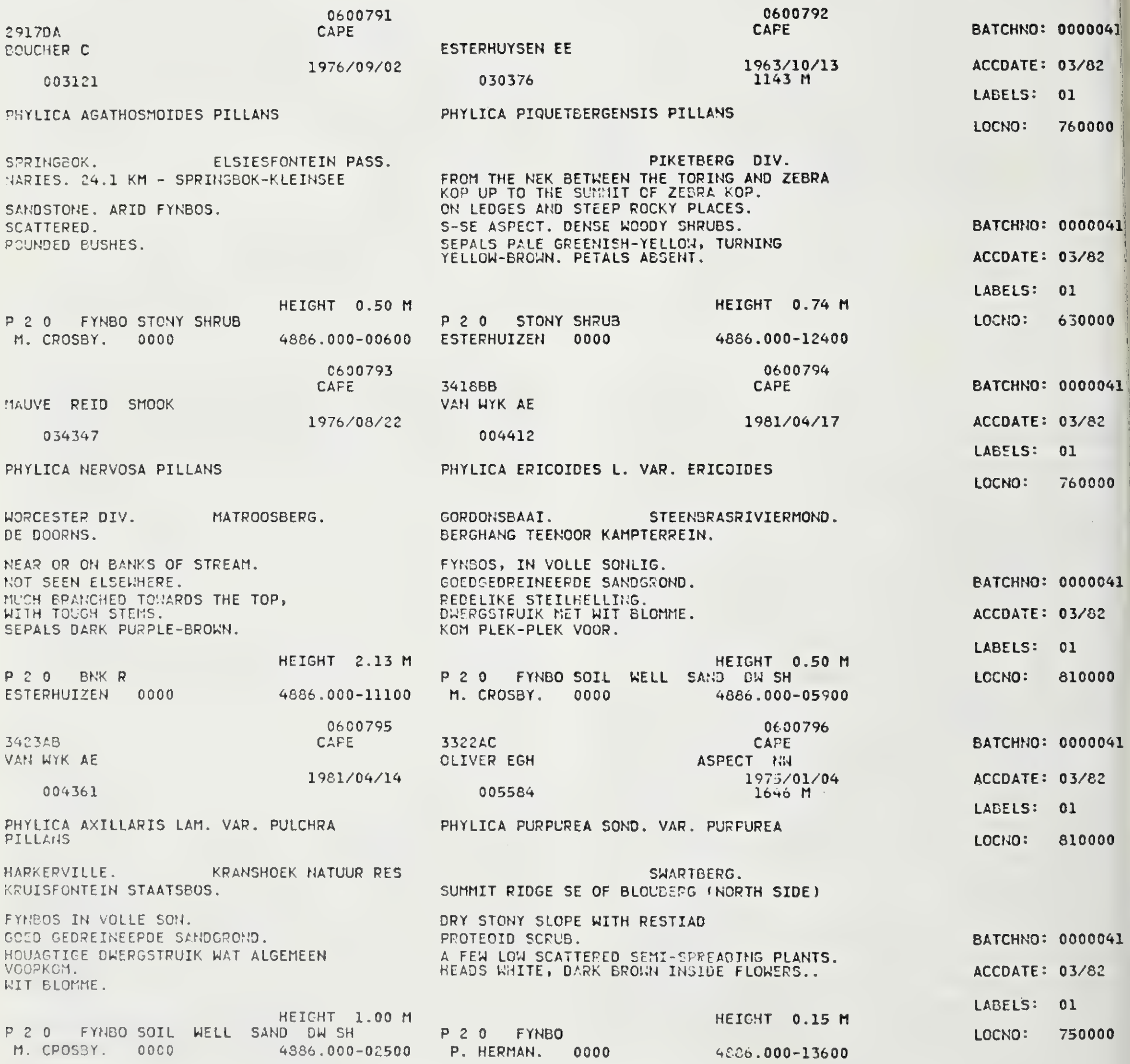
The information stored in the data sets is accessible by the Burroughs information retrieval package (INQUIRY). This system is suitable for research at the Institute, because it is an on-line system available on remote terminals. Information requested from the data bank can be displayed on terminals or printed out at the Institute. In addition, the possible uses of the system are increased because the requested data can be sorted, and the format of the printout varied to suit particular purposes. There are four major areas of information retrieval available from the herbarium data bank. A few of the possibilities are listed below as examples.

3.1 *Collectors information*

Specific information relating to a collectors record-keeping, including register of his collecting localities (Fig. 4), lists of collected specimens reported by specimen number (Fig. 5) or selected groups of plants (Fig. 6).

3.2 *Herbarium curation*

In addition to specimen label production by the new system, INQUIRY provides lists of specimens



```
                                 0600791                                      0600792
2917DA                          CAPE                                         CAPE                BATCHNO: 0000041
BOUCHER C                                    ESTERHUYSEN EE
                               1976/09/02                                  1963/10/13            ACCDATE: 03/82
    003121                                       030376                    1143 M
                                                                                                 LABELS:  01
PHYLICA AGATHOSMOIDES PILLANS                PHYLICA PIQUETBERGENSIS PILLANS
                                                                                                 LOCNO:   760000

SPRINGBOK.              ELSIESFONTEIN PASS.                      PIKETBERG  DIV.
NARIES. 24.1 KM - SPRINGBOK-KLEINSEE         FROM THE NEK BETWEEN THE TORING AND ZEBRA
                                             KOP UP TO THE SUMMIT OF ZEBRA KOP.
SANDSTONE. ARID FYNBOS.                      ON LEDGES AND STEEP ROCKY PLACES.
SCATTERED.                                   S-SE ASPECT. DENSE WOODY SHRUBS.                    BATCHNO: 0000041
ROUNDED BUSHES.                              SEPALS PALE GREENISH-YELLOW, TURNING
                                             YELLOW-BROWN. PETALS ABSENT.                        ACCDATE: 03/82

                                                                                                 LABELS:  01
                            HEIGHT  0.50 M                              HEIGHT  0.74 M
P 2 0   FYNBO STONY SHRUB                    P 2 0   STONY SHRUB                                 LOCNO:   630000
 M. CROSBY.   0000          4886.000-00600   ESTERHUIZEN   0000         4886.000-12400

                                 0600793                                      0600794
                                CAPE         3418BB                          CAPE                BATCHNO: 0000041
MAUVE  REID  SMOOK                           VAN WYK AE
                               1976/08/22                                  1981/04/17            ACCDATE: 03/82
    034347                                       004412
                                                                                                 LABELS:  01
PHYLICA NERVOSA PILLANS                      PHYLICA ERICOIDES L. VAR. ERICOIDES
                                                                                                 LOCNO:   760000

WORCESTER DIV.          MATROOSBERG.         GORDONSBAAI.            STEENBRASRIVIERMOND.
DE DOORNS.                                   BERGHANG TEENOOR KAMPTERREIN.

NEAR OR ON BANKS OF STREAM.                  FYNBOS, IN VOLLE SONLIG.
NOT SEEN ELSEWHERE.                          GOEDGEDREINEERDE SANDGROND.                         BATCHNO: 0000041
MUCH BRANCHED TOWARDS THE TOP,               REDELIKE STEILHELLING.
WITH TOUGH STEMS.                            DWERGSTRUIK MET WIT BLOMME.                         ACCDATE: 03/82
SEPALS DARK PURPLE-BROWN.                    KOM PLEK-PLEK VOOR.
                                                                                                 LABELS:  01
                            HEIGHT  2.13 M                              HEIGHT  0.50 M
P 2 0   BNK R                                P 2 0   FYNBO SOIL  WELL  SAND  DW SH               LOCNO:   810000
ESTERHUIZEN   0000          4886.000-11100    M. CROSBY.   0000         4886.000-05900

                                 0600795                                      0600796
3423AB                          CAPE         3322AC                          CAPE                BATCHNO: 0000041
VAN WYK AE                                   OLIVER EGH                 ASPECT  NW
                               1981/04/14                                  1975/01/04            ACCDATE: 03/82
    004361                                       005584                    1646 M
                                                                                                 LABELS:  01
PHYLICA AXILLARIS LAM. VAR. PULCHRA          PHYLICA PURPUREA SOND. VAR. PURPUREA
PILLANS                                                                                          LOCNO:   810000

HARKERVILLE.            KRANSHOEK NATUUR RES                     SWARTBERG.
KRUISFONTEIN STAATSBOS.                      SUMMIT RIDGE SE OF BLOUBERG (NORTH SIDE)

FYNBOS IN VOLLE SON.                         DRY STONY SLOPE WITH RESTIAD
GOED GEDREINEERDE SANDGROND.                 PROTEOID SCRUB.                                     BATCHNO: 0000041
HOUAGTIGE DWERGSTRUIK WAT ALGEMEEN           A FEW LOW SCATTERED SEMI-SPREADING PLANTS.
VOORKOM.                                     HEADS WHITE, DARK BROWN INSIDE FLOWERS..            ACCDATE: 03/82
WIT BLOMME.
                                                                                                 LABELS:  01
                            HEIGHT  1.00 M                              HEIGHT  0.15 M
P 2 0   FYNBO SOIL  WELL  SAND  DW SH        P 2 0   FYNBO                                       LOCNO:   750000
 M. CROSBY.   0000          4886.000-02500    P. HERMAN.   0000         4886.000-13600
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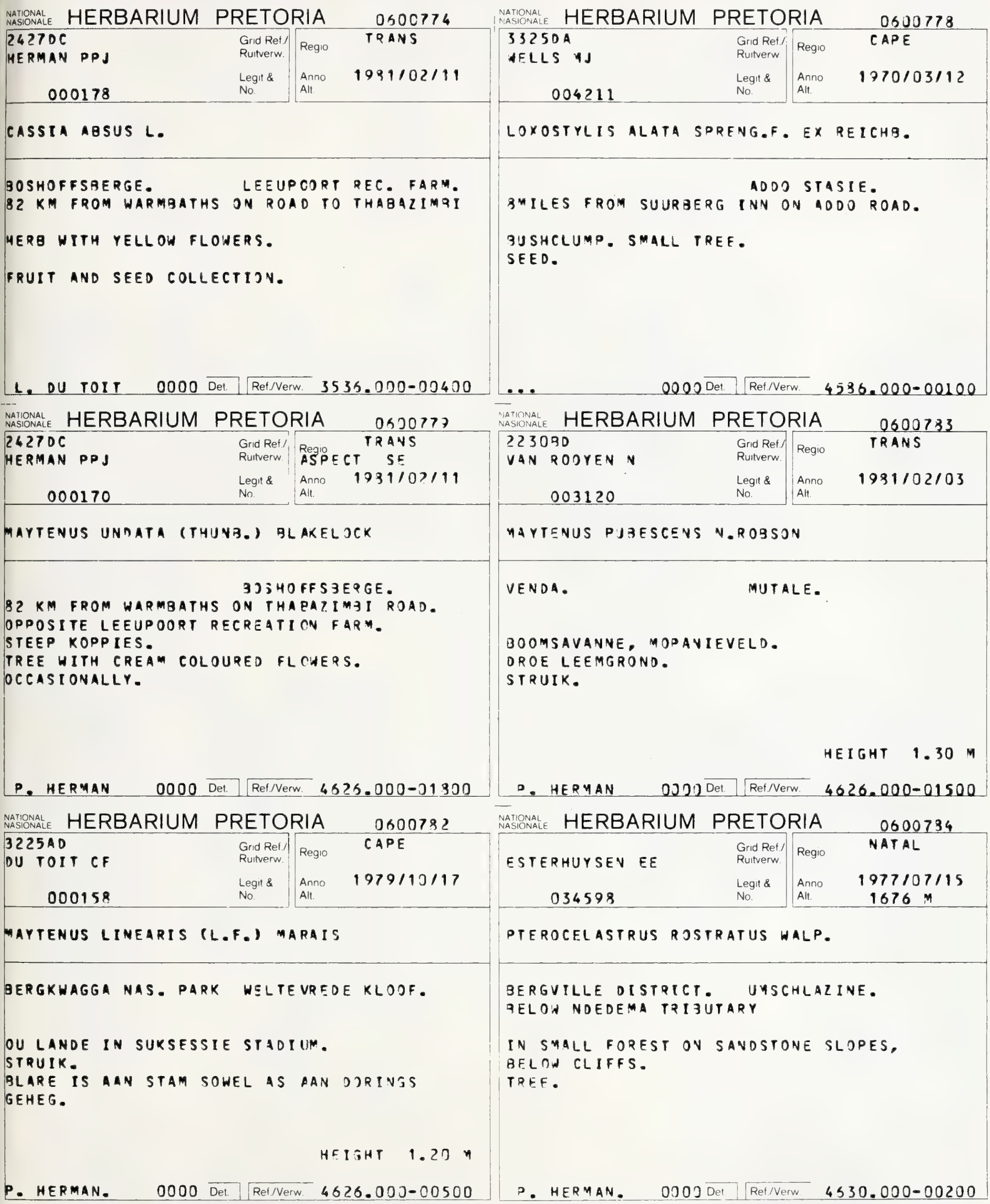
FIG. 2—'Counterfeit' specimen label, for proofreading by the collector or herbarium staff.



NATIONAL NASIONALE HERBARIUM PRETORIA 0600774
2427DC Grid Ref./Ruitverw.
HERMAN PPJ
000178 Legit & No.
Regio TRANS
Anno 1981/02/11
Alt.
CASSIA ABSUS L.
BOSHOFFSBERGE. LEEUPOORT REC. FARM.
82 KM FROM WARMBATHS ON ROAD TO THABAZIMBI
HERB WITH YELLOW FLOWERS.
FRUIT AND SEED COLLECTION.
L. DU TOIT 0000 Det. Ref./Verw. 3536.000-00400

NATIONAL NASIONALE HERBARIUM PRETORIA 0600778
3325DA Grid Ref./Ruitverw.
WELLS MJ
004211 Legit & No.
Regio CAPE
Anno 1970/03/12
Alt.
LOXOSTYLIS ALATA SPRENG.F. EX REICHB.
ADDO STASIE.
8MILES FROM SUURBERG INN ON ADDO ROAD.
BUSHCLUMP. SMALL TREE.
SEED.
... 0000 Det. Ref./Verw. 4536.000-00100

NATIONAL NASIONALE HERBARIUM PRETORIA 0600779
2427DC Grid Ref./Ruitverw.
HERMAN PPJ
000170 Legit & No.
Regio TRANS
ASPECT SE
Anno 1981/02/11
Alt.
MAYTENUS UNDATA (THUNB.) BLAKELOCK
BOSHOFFSBERGE.
82 KM FROM WARMBATHS ON THABAZIMBI ROAD.
OPPOSITE LEEUPOORT RECREATION FARM.
STEEP KOPPIES.
TREE WITH CREAM COLOURED FLOWERS.
OCCASIONALLY.
P. HERMAN 0000 Det. Ref./Verw. 4626.000-01800

NATIONAL NASIONALE HERBARIUM PRETORIA 0600783
2230BD Grid Ref./Ruitverw.
VAN ROOYEN N
003120 Legit & No.
Regio TRANS
Anno 1981/02/03
Alt.
MAYTENUS PUBESCENS N.ROBSON
VENDA. MUTALE.
BOOMSAVANNE, MOPANIEVELD.
DROE LEEMGROND.
STRUIK.
HEIGHT 1.30 M
P. HERMAN 0000 Det. Ref./Verw. 4626.000-01500

NATIONAL NASIONALE HERBARIUM PRETORIA 0600782
3225AD Grid Ref./Ruitverw.
DU TOIT CF
000158 Legit & No.
Regio CAPE
Anno 1979/10/17
Alt.
MAYTENUS LINEARIS (L.F.) MARAIS
BERGKWAGGA NAS. PARK WELTEVREDE KLOOF.
OU LANDE IN SUKSESSIE STADIUM.
STRUIK.
BLARE IS AAN STAM SOWEL AS AAN DORINGS
GEHEG.
HEIGHT 1.20 M
P. HERMAN. 0000 Det. Ref./Verw. 4626.000-00500

NATIONAL NASIONALE HERBARIUM PRETORIA 0600784
Grid Ref./Ruitverw.
ESTERHUYSEN EE
034598 Legit & No.
Regio NATAL
Anno 1977/07/15
Alt. 1676 M
PTEROCELASTRUS ROSTRATUS WALP.
BERGVILLE DISTRICT. UMSCHLAZINE.
BELOW NDEDEMA TRIBUTARY
IN SMALL FOREST ON SANDSTONE SLOPES,
BELOW CLIFFS.
TREE.
P. HERMAN. 0000 Det. Ref./Verw. 4630.000-00200

FIG. 3.—Specimen labels.

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COLLECTOR                               LOCNO    GRID     REGION     DATE      MAJOR                     MINOR                  REGNO
==================================================================================================================================

SMOOK L                                 81-0030  2528BD   TRANS   1981/03/17   KWANDEBELE                FARM GEMSBOKFONTEIN     94
                                        AT FARMHOUSE  AREA DISTURBED

SMOOK L                                 81-0031  2528BB   TRANS   1981/03/17   KWANDEBELE                FARM BOEKENHOUTFONT.    94
                                        AT FARM BOUNDARY.

SMOOK L                                 81-0032  2528BD   TRANS   1981/03/17   KWANDEBELE                BOEKENHOUTFONTEIN FR    94
                                        AT RIVER

SMOOK L                                 81-0033  2528BD   TRANS   1981/03/17   KWANDEBELE                FARM BOEKENHOUFONT.     94
                                        CLIFF ABOVE RIVER.

SMOOK L                                 81-0034  2528BD   TRANS   1981/03/17   KWANDEBELE                FARM GEMSBOKFONTEIN     94
                                        LOCAL AIRSTRIP

SMOOK L                                 81-0035  2529AC   TRANS   1981/03/18   KWANDEBELE                FARM GOEDEREDE.         94

SMOOK L                                 81-0037  3025BB   O F S   1981/03/31   TROMPSBURG                TROMPSBURG.             94
                                        TOWN.

SMOOK L                                 81-0040  3025CA   CAPE    1981/04/01   COLESBERG.                COLESBERG.              94
                                        5 KM OUT OF COLESBERG ON ROAD TO        STEYNSBURG.

SMOOK L                                 81-0041  3025CA   CAPE    1981/04/01   COLESBERG                 COLESBERG.              94
                                        7 KM FROM COLESBERG ON ROAD TO          STORMFONTEIN

SMOOK L                                 81-0042  3025CD   CAPE    1981/04/01   COLESBERG.                FARM HOLLE RIVER.       94
                                        20 KM FROM COLESBERG ON ROAD TO         STORMFONTEIN

SMOOK L                                 81-0043  3025DA   CAPE    1981/04/01   COLESBERG.                BULTFONTEIN.            94
                                        42 KM EAST OF COLESBERG ON BULTFONTEIN RD

SMOOK L                                 81-0044  3025DC   CAPE    1981/04/02   COLESBERG                 FARM BOESMANSPOORT.     94
                                        75 KM S E OF COLESBERG ON ROAD TO        BULTFONTEIN-STEYNSBURG.

SMOOK L                                 81-0045  3125AB   CAPE    1981/04/02   COLESBERG                 FARM WELTEVREDE         94
                                        HAASFONTEINBERG 50 KM N E  OF NOUPOORT.
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FIG. 4.—Collector's register of localities.

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                                                     COLLECTOR'S REGISTER FOR R E MAGILL

                                                                  11/27/81

 SPMNO NAME                                               YR  MO DY REGION GRID   MAJOR                MINOR
--------- ----------------------------------------------- ---- -- -- ------ ------ -------------------- ------------
     3340 MACROCOMA TENUE (HOOK. & GREV.) VITT            1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3341 BRYUM BILLARDIERI SCHWAEGR.                     1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3342 TRICHOSTOMUM BRACHYDONTIUM BRUCH.               1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3343 MACROCOMA TENUE (HOOK. & GREV.) VITT            1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3345 FORSSTROEMIA PRODUCTA (HORNSCH.) PAR.           1977  2  2 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3346 PAPILLARIA AFRICANA (C. MUELL.) JAEG.           1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3347 PILOTRICHELLA PANDURAEFOLIA (C. MUELL.) JA      1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3347 PAPILLARIA AFRICANA (C. MUELL.) JAEG.           1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3348 BRACHYMENIUM PULCHRUM HOOK.                     1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3350 TRICHOSTOMUM BRACHYDONTIUM BRUCH.               1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3352 PAPILLARIA AFRICANA (C. MUELL.) JAEG.           1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3353 TRICHOSTOMUM BRACHYDONTIUM BRUCH.               1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3354 SEMATOPHYLLUM BRACHYCARPUM (HAMPE) BROTH.       1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3355 SEMATOPHYLLUM BRACHYCARPUM (HAMPE) BROTH.       1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3356 CAMPYLOPUS SP.                                  1977  2  3 TRANS  2430CA SEKHUKHUNELAND       STEELPOORT
     3357 BRYUM CAPILLARE HEDW.                           1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3359 MACROCOMA TENUE (HOOK. & GREV.) VITT            1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3360 BRYUM SP.                                       1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3361 SEMATOPHYLLUM BRACHYCARPUM (HAMPE) BROTH.       1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3362 PAPILLARIA AFRICANA (C. MUELL.) JAEG.           1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3364 CAMPYLOPUS SP.                                  1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3364 CAMPYLOPUS SP.                                  1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3365 AULACOPILUM TRICHOPHYLLUM AONGSTR.              1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3366 PTYCHOMITRIUM SUBCRISPATUM THER. & P. VARD      1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3367 BRAUNIA SECUNDA (HOOK.) B.S.G.                  1977  2  2 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3368 MACROCOMA TENUE (HOOK. & GREV.) VITT            1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3369 GRIMMIA APOCARPA HEDW.                          1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3371 BRYUM BILLARDIERI SCHWAEGR.                     1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3372 MACROCOMA TENUE (HOOK. & GREV.) VITT            1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3375 LEPTODON SMITHII (HEDW.) WEB. & MOHR            1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3376 FISSIDENS GLAUCESCENS HORNSCH.                  1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3377 TORTULA PAGORUM (MILDE) DE NOT                  1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3378 LEPTODON SMITHII (HEDW.) WEB. & MOHR            1977  2  3 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3379 TORTULA PRINCEPS DE NOT.                        1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3379 TORTULA PRINCEPS DE NOT.                        1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3380 BRACHYMENIUM ACUMINATUM HARV. IN HOOK.          1977  2  3 TRANS  2430CA SEKHUKHUNELAND       LULUBERG
     3381 LEUCODON MARITIMUS (HOOK.) WIJK & MARG.         1977  2  2 TRANS  2430CA SEKUKUNILAND         LULU MTS.
     3385 CAMPYLOPUS INTROFLEXUS (HEDW.) BRID.            1977  2  4 TRANS  2529D
     3386 TRICHOSTOMUM BRACHYDONTIUM BRUCH.               1977  2  4 TRANS
     3387 CAMPYLOPUS INTROFLEXUS (HEDW.) BRID.            1977  2  4 TRANS  2529
     3389 CAMPYLOPUS INTROFLEXUS (HEDW.) BRID.            1977  2  4 TRANS
     3390 TRICHOSTOMUM BRACHYDONTIUM BRUCH.               1977  2  4 TRANS
     3393 TRICHOSTOMUM BRACHYDONTIUM BRUCH.               1977  1 31 TRANS  2430CC MAARTENSHOOP         GROOT DUARIVER
     3395 TRICHOSTOMUM BRACHYDONTIUM BRUCH.               1977  1 31 TRANS  2430CC MAARTENSHOOP         GROOT DUARIVER
     3398 SEMATOPHYLLUM BRACHYCARPUM (HAMPE) BROTH.       1977  3 10 TRANS  2630AB
     3400 MICROCAMPYLOPUS PERPUSILLUS (MITT.) BROTH.      1977  3 10 TRANS  2630AB
     3400 MICROCAMPYLOPUS PERPUSILLUS (MITT.) BROTH.      1977  3 10 TRANS  2630AB
     3401 LEPTODONTIUM BRACHYPHYLLUM BROTH. & THER.       1977  3 10 TRANS  2630AB
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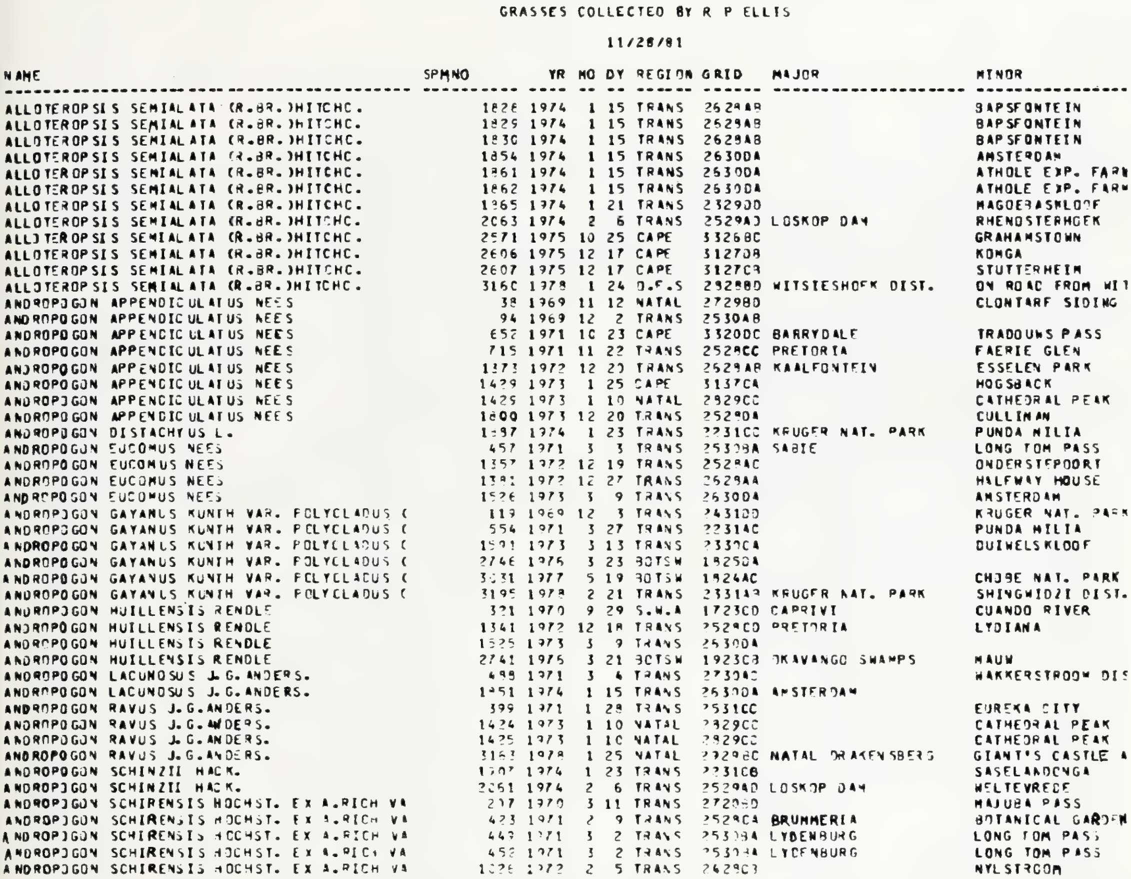
FIG. 5.—Collector's register of specimens.



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                                                    GRASSES COLLECTED BY R P ELLIS

                                                              11/28/81

NAME                                          SPMNO        YR MO DY REGION GRID   MAJOR                MINOR
--------------------------------------------- ---------- ---- -- -- ------ ------ -------------------- ----------------
ALLOTEROPSIS SEMIALATA (R.BR.)HITCHC.               1826 1974  1 15 TRANS  2629AB                      BAPSFONTEIN
ALLOTEROPSIS SEMIALATA (R.BR.)HITCHC.               1829 1974  1 15 TRANS  2629AB                      BAPSFONTEIN
ALLOTEROPSIS SEMIALATA (R.BR.)HITCHC.               1830 1974  1 15 TRANS  2629AB                      BAPSFONTEIN
ALLOTEROPSIS SEMIALATA (R.BR.)HITCHC.               1854 1974  1 15 TRANS  2630DA                      AMSTERDAM
ALLOTEROPSIS SEMIALATA (R.BR.)HITCHC.               1861 1974  1 15 TRANS  2630DA                      ATHOLE EXP. FARM
ALLOTEROPSIS SEMIALATA (R.BR.)HITCHC.               1862 1974  1 15 TRANS  2630DA                      ATHOLE EXP. FARM
ALLOTEROPSIS SEMIALATA (R.BR.)HITCHC.               1965 1974  1 21 TRANS  2329DD                      MAGOEBASKLOOF
ALLOTEROPSIS SEMIALATA (R.BR.)HITCHC.               2063 1974  2  6 TRANS  2529AD LOSKOP DAM           RHENOSTERHOEK
ALLOTEROPSIS SEMIALATA (R.BR.)HITCHC.               2571 1975 10 25 CAPE   3326BC                      GRAHAMSTOWN
ALLOTEROPSIS SEMIALATA (R.BR.)HITCHC.               2606 1975 12 17 CAPE   3127DB                      KOMGA
ALLOTEROPSIS SEMIALATA (R.BR.)HITCHC.               2607 1975 12 17 CAPE   3127CB                      STUTTERHEIM
ALLOTEROPSIS SEMIALATA (R.BR.)HITCHC.               3160 1978  1 24 O.F.S  2928BD WITSIESHOEK DIST.    ON ROAD FROM WIT
ANDROPOGON APPENDICULATUS NEES                        38 1969 11 12 NATAL  2729BD                      CLONTARF SIDING
ANDROPOGON APPENDICULATUS NEES                        94 1969 12  2 TRANS  2530AB
ANDROPOGON APPENDICULATUS NEES                       652 1971 10 23 CAPE   3320DC BARRYDALE            TRADOUWS PASS
ANDROPOGON APPENDICULATUS NEES                       715 1971 11 22 TRANS  2528CC PRETORIA             FAERIE GLEN
ANDROPOGON APPENDICULATUS NEES                      1373 1972 12 20 TRANS  2629AB KAALFONTEIN          ESSELEN PARK
ANDROPOGON APPENDICULATUS NEES                      1429 1973  1 25 CAPE   3137CA                      HOGSBACK
ANDROPOGON APPENDICULATUS NEES                      1425 1973  1 10 NATAL  2929CC                      CATHEDRAL PEAK
ANDROPOGON APPENDICULATUS NEES                      1800 1973 12 20 TRANS  2528DA                      CULLINAN
ANDROPOGON DISTACHYUS L.                            1397 1974  1 23 TRANS  2231CC KRUGER NAT. PARK     PUNDA MILIA
ANDROPOGON EUCOMUS NEES                              457 1971  3  3 TRANS  2530BA SABIE                LONG TOM PASS
ANDROPOGON EUCOMUS NEES                             1357 1972 12 19 TRANS  2528AC                      ONDERSTEPOORT
ANDROPOGON EUCOMUS NEES                             1381 1972 12 27 TRANS  2628AA                      HALFWAY HOUSE
ANDROPOGON EUCOMUS NEES                             1526 1973  3  9 TRANS  2630DA                      AMSTERDAM
ANDROPOGON GAYANUS KUNTH VAR. POLYCLADUS (           119 1969 12  3 TRANS  2431DD                      KRUGER NAT. PARK
ANDROPOGON GAYANUS KUNTH VAR. POLYCLADUS (           554 1971  3 27 TRANS  2231AC                      PUNDA MILIA
ANDROPOGON GAYANUS KUNTH VAR. POLYCLADUS (          1591 1973  3 13 TRANS  2330CA                      DUIWELSKLOOF
ANDROPOGON GAYANUS KUNTH VAR. POLYCLADUS (          2746 1976  3 23 BOTSW  1825DA
ANDROPOGON GAYANUS KUNTH VAR. POLYCLADUS (          3031 1977  5 19 BOTSW  1824AC                      CHOBE NAT. PARK
ANDROPOGON GAYANUS KUNTH VAR. POLYCLADUS (          3195 1978  2 21 TRANS  2331AB KRUGER NAT. PARK     SHINGWIDZI DIST.
ANDROPOGON HUILLENSIS RENDLE                         321 1970  9 29 S.W.A  1723CD CAPRIVI              CUANDO RIVER
ANDROPOGON HUILLENSIS RENDLE                        1341 1972 12 18 TRANS  2528CD PRETORIA             LYDIANA
ANDROPOGON HUILLENSIS RENDLE                        1525 1973  3  9 TRANS  2630DA
ANDROPOGON HUILLENSIS RENDLE                        2741 1975  3 21 BOTSW  1923CB OKAVANGO SWAMPS      MAUW
ANDROPOGON LACUNOSUS J.G.ANDERS.                     499 1971  3  4 TRANS  2730AC                      WAKKERSTROOM DIS
ANDROPOGON LACUNOSUS J.G.ANDERS.                    1951 1974  1 15 TRANS  2630DA AMSTERDAM
ANDROPOGON RAVUS J.G.ANDERS.                         399 1971  1 28 TRANS  2531CC                      EUREKA CITY
ANDROPOGON RAVUS J.G.ANDERS.                        1424 1973  1 10 NATAL  2929CC                      CATHEDRAL PEAK
ANDROPOGON RAVUS J.G.ANDERS.                        1425 1973  1 10 NATAL  2929CC                      CATHEDRAL PEAK
ANDROPOGON RAVUS J.G.ANDERS.                        3163 1978  1 25 NATAL  2929BC NATAL DRAKENSBERG    GIANT'S CASTLE A
ANDROPOGON SCHINZII HACK.                           1707 1974  1 23 TRANS  2231CB                      SASELANDONGA
ANDROPOGON SCHINZII HACK.                           2261 1974  2  6 TRANS  2529AD LOSKOP DAM           WELTEVREDE
ANDROPOGON SCHIRENSIS HOCHST. EX A.RICH VA           217 1970  3 11 TRANS  2729BD                      MAJUBA PASS
ANDROPOGON SCHIRENSIS HOCHST. EX A.RICH VA           423 1971  2  9 TRANS  2528CA BRUMMERIA            BOTANICAL GARDEN
ANDROPOGON SCHIRENSIS HOCHST. EX A.RICH VA           443 1971  3  2 TRANS  2530BA LYDENBURG            LONG TOM PASS
ANDROPOGON SCHIRENSIS HOCHST. EX A.RICH VA           452 1971  3  2 TRANS  2530BA LYDENBURG            LONG TOM PASS
ANDROPOGON SCHIRENSIS HOCHST. EX A.RICH VA          1026 1972  2  5 TRANS  2428CB                      NYLSTROOM
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FIG. 6.—Specimens of a particular collector in one plant family.

that are useful in various curatorial duties such as type registers (Fig. 7), lists of specimens sorted by collectors for loan forms (Fig. 8), or catalogues of taxa (Fig. 9).

3.3 *Floristic and taxonomic research*

This covers specimen data specific to the distribution of taxa. The system provides an important tool to research on regional (Fig. 10) or local floras by providing lists of specimens from requested areas. Other possibilities include sorting specimens by altitude (Fig. 11) for zonal distribution data or producing lists of grid references (Fig. 12) for use in production of distribution maps for publication (Fig. 13) or research purposes (Fig. 14).

3.4 *Specimen-related taxon data*

The information encoded in sections C and D of the collecting form can be extremely important in gaining additional information for taxonomic or floristic research. Each of the fields can be used in connection with taxon numbers to produce lists of specimens that fall within specific categories such as succulent Compositae, aquatic bryophytes (Fig. 15),

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                                                          TYPE SPECIMENS OF HERMANNIA IN PRE

                                                                       12/08/81

 GENUS  SPECIES NAME                                       COLLECTOR       SPMNO       PRENO TYPES
------- ------- ------------------------------------------ -------------- ---------- ------- -----
5056000   11100 HERMANNIA GLABRATA L.F.                    THUNBERG CP    PRE 48009  293854 T
5056000   11100 HERMANNIA GLABRATA L.F.                    THUNBERG CP    PRE 48010  293855 T
5056000   11300 HERMANNIA GLANDULIGERA K.SCHUM.            RAUTANEN               78  303267 T
5056000   11300 HERMANNIA GLANDULIGERA K.SCHUM.            SCHINZ H              600  303266 T
5056000   11700 HERMANNIA GRACILIS ECKL. & ZEYH.           ECKLON  ZEYHER        358  320185 T
5056000   11900 HERMANNIA GRANDIFLORA AIT.                 BURCHELL WJ          1536  300974 T
5056000   12000 HERMANNIA GRANDIFOLIA N.E.BR.              GALPIN EE             940  298121 T
5056000   12300 HERMANNIA GRISEA SCHINZ                    SCHLECHTER R         4631  304613 T
5056000   12500 HERMANNIA GROSSULARIFOLIA L.               PRE            PRE 48449  300956 H
5056000   12500 HERMANNIA GROSSULARIFOLIA L.               PRE            LH 854.14  300955 H
5056000   12500 HERMANNIA GROSSULARIFOLIA L.               DREGE          PRE 48452  300957 P
5056000   12700 HERMANNIA GUERKEANA K.SCHUM.               SCHINZ H              601  304649 T
5056000   12700 HERMANNIA GUERKEANA K.SCHUM.               DINTER K              355  304650 T
5056000   12900 HERMANNIA HELIANTHEMUM K.SCHUM.            MARLOTH R            1237  307537 L
5056000   13100 HERMANNIA HELICOIDEA VERDOORN              PILLANS NS           9063  322652 H
5056000   13300 HERMANNIA HETEROPHYLLA (CAV.) THUNB. SUBSP THUNBERG CP    PRE 47854  289184 H
5056000   13300 HERMANNIA HETEROPHYLLA (CAV.) THUNB. SUBSP SONNERAT P      JU 12483  289183 H
5056000   14700 HERMANNIA INCANA CAV.                      CELS D                473  317110 H
5056000   14700 HERMANNIA INCANA CAV.                      ECKLON  ZEYHER        333  317116 S
5056000   14700 HERMANNIA INCANA CAV.                      DREGE JF             7300  317113 T
5056000   14700 HERMANNIA INCANA CAV.                      MASSON         PRE 49280  317115 T
5056000   14700 HERMANNIA INCANA CAV.                      WILLDENOW           12308  317111 T
5056000   14700 HERMANNIA INCANA CAV.                      DREGE JF             7302  317114 T
5056000   14700 HERMANNIA INCANA CAV.                      DREGE JF             7301  317112 T
5056000   14900 HERMANNIA INVOLUCRATA CAV.                 THUNBERG       PRE 51810  354811 T
5056000   14900 HERMANNIA INVOLUCRATA CAV.                 THUNBERG CP    PRE 39657  323892 T
5056000   14900 HERMANNIA INVOLUCRATA CAV.                 ECKLON  ZEYHER        346  323893 T
5056000   15300 HERMANNIA JOHANSSENII N.E.BR.              JOHANSSEN Y    PRE 49247  316753 H
5056000   15400 HERMANNIA JOUBERTIANA HARV.                JOUBERT H      PRE 49706  325055 T
5056000   15500 HERMANNIA JUTTAE DINTER & ENGL.            DINTER K             8321  326055 T
5056000   16200 HERMANNIA LEUCANTHA SCHLECHTD.             SCHLECHTER          11456  290323 H
5056000   16200 HERMANNIA LEUCANTHA SCHLECHTD.             SCHLECHTER          11456  290322 S
5056000   16500 HERMANNIA LINEARIFOLIA HARV.               BARBER          PRE 9230  303492 S
5056000   16500 HERMANNIA LINEARIFOLIA HARV.               DREGE          PRE 48750  303493 T
5056000   16700 HERMANNIA LINIFOLIA BURM.F.                ECKLON  ZEYHER        404  310918 H
5056000   16700 HERMANNIA LINIFOLIA BURM.F.                PRE             PRE 5189  310917 T
5056000   16900 HERMANNIA LINNAEOIDES (BURCH.) K.SCHUM.    BURCHELL WJ          1878  293819 H
5056000   17000 HERMANNIA LITTORALIS VERDOORN              ACOCKS JPH          15205  301984 T
5056000   17300 HERMANNIA MACRA SCHLTR.                    SCHLECHTER M          106  326045 S
5056000   17300 HERMANNIA MACRA SCHLTR.                    SCHLECHTER R        11403  325044 S
5056000   17500 HERMANNIA MALVAEFOLIA N.E.BR.              EVANS MS               55  296533 T
5056000   17700 HERMANNIA MARGINATA PILLANS                DREGE          PRE 48020  293879 H
5056000   17700 HERMANNIA MARGINATA PILLANS                ZEYHER CL             133  293881 T
5056000   17700 HERMANNIA MARGINATA PILLANS                ZEYHER CL             133  293880 T
5056000   17900 HERMANNIA MERXMUELLERI H.FRIEDRICH         MERXMULLER  GI       1664  302048 T
5056000   18300 HERMANNIA MICRANTHA ADAMSON                ADAMSON RS           2618  323977 T
5056000   18500 HERMANNIA MICROPETALA HARV.                SCHLECHTER R        11576  304668 T
5056000   18500 HERMANNIA MICROPETALA HARV.                FORBES          PRE 9227  304667 T
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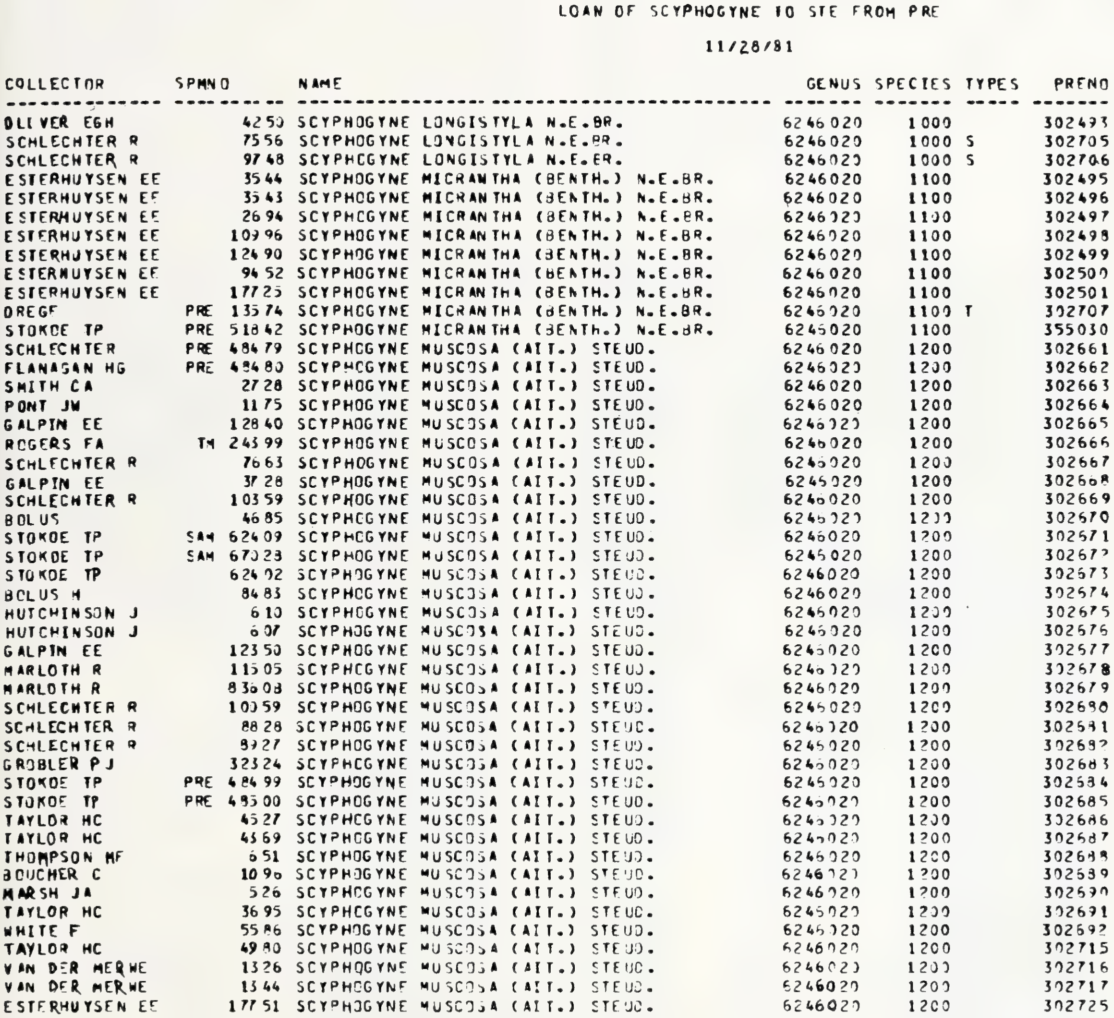
FIG. 7.—List of type specimens in a genus.



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                                                  LOAN OF SCYPHOGYNE TO STE FROM PRE

                                                              11/28/81

COLLECTOR        SPMNO       NAME                                              GENUS  SPECIES TYPES   PRENO
-------------- --------- ----------------------------------------------- ------- ------- -----  -------
OLIVER EGH          4250 SCYPHOGYNE LONGISTYLA N.E.BR.                    6246020    1000           302493
SCHLECHTER R        7556 SCYPHOGYNE LONGISTYLA N.E.BR.                    6246020    1000 S         302705
SCHLECHTER R        9748 SCYPHOGYNE LONGISTYLA N.E.BR.                    6246020    1000 S         302706
ESTERHUYSEN EE      3544 SCYPHOGYNE MICRANTHA (BENTH.) N.E.BR.            6246020    1100           302495
ESTERHUYSEN EE      3543 SCYPHOGYNE MICRANTHA (BENTH.) N.E.BR.            6246020    1100           302496
ESTERHUYSEN EE      2694 SCYPHOGYNE MICRANTHA (BENTH.) N.E.BR.            6246020    1100           302497
ESTERHUYSEN EE     10996 SCYPHOGYNE MICRANTHA (BENTH.) N.E.BR.            6246020    1100           302498
ESTERHUYSEN EE     12490 SCYPHOGYNE MICRANTHA (BENTH.) N.E.BR.            6246020    1100           302499
ESTERHUYSEN EE      9452 SCYPHOGYNE MICRANTHA (BENTH.) N.E.BR.            6246020    1100           302500
ESTERHUYSEN EE     17725 SCYPHOGYNE MICRANTHA (BENTH.) N.E.BR.            6246020    1100           302501
DREGE          PRE 13574 SCYPHOGYNE MICRANTHA (BENTH.) N.E.BR.            6246020    1100 T         302707
STOKOE TP      PRE 51842 SCYPHOGYNE MICRANTHA (BENTH.) N.E.BR.            6246020    1100           355030
SCHLECHTER     PRE 48479 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302661
FLANAGAN HG    PRE 48480 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302662
SMITH CA            2728 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302663
PONT JW             1175 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302664
GALPIN EE          12840 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302665
ROGERS FA       TM 24399 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302666
SCHLECHTER R        7663 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302667
GALPIN EE           3728 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302668
SCHLECHTER R       10359 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302669
BOLUS               4685 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302670
STOKOE TP      SAM 62409 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302671
STOKOE TP      SAM 67028 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302672
STOKOE TP          62402 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302673
BOLUS H             8483 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302674
HUTCHINSON J         610 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302675
HUTCHINSON J         607 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302676
GALPIN EE          12350 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302677
MARLOTH R          11505 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302678
MARLOTH R          83608 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302679
SCHLECHTER R       10059 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302680
SCHLECHTER R        8828 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302681
SCHLECHTER R        8927 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302682
GROBLER PJ         32324 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302683
STOKOE TP      PRE 48499 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302684
STOKOE TP      PRE 48500 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302685
TAYLOR HC           4527 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302686
TAYLOR HC           4569 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302687
THOMPSON MF          651 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302688
BOUCHER C           1096 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302689
MARSH JA             526 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302690
TAYLOR HC           3695 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302691
WHITE F             5586 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302692
TAYLOR HC           4980 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302715
VAN DER MERWE       1326 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302716
VAN DER MERWE       1344 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302717
ESTERHUYSEN EE     17751 SCYPHOGYNE MUSCOSA (AIT.) STEUD.                 6246020    1200           302725
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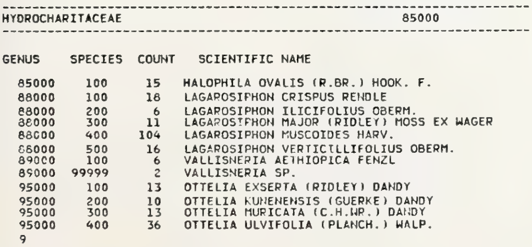
FIG. 8.—List of specimens to be sent on loan.



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HYDROCHARITACEAE                                     85000
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GENUS    SPECIES  COUNT   SCIENTIFIC NAME

  85000     100     15   HALOPHILA OVALIS (R.BR.) HOOK. F.
  88000     100     18   LAGAROSIPHON CRISPUS RENDLE
  88000     200      6   LAGAROSIPHON ILICIFOLIUS OBERM.
  88000     300     11   LAGAROSIPHON MAJOR (RIDLEY) MOSS EX WAGER
  88000     400    104   LAGAROSIPHON MUSCOIDES HARV.
  88000     500     16   LAGAROSIPHON VERTICILLIFOLIUS OBERM.
  89000     100      6   VALLISNERIA AETHIOPICA FENZL
  89000   99999      2   VALLISNERIA SP.
  95000     100     13   OTTELIA EXSERTA (RIDLEY) DANDY
  95000     200     10   OTTELIA KUNENENSIS (GUERKE) DANDY
  95000     300     13   OTTELIA MURICATA (C.H.WR.) DANDY
  95000     400     36   OTTELIA ULVIFOLIA (PLANCH.) WALP.
   9
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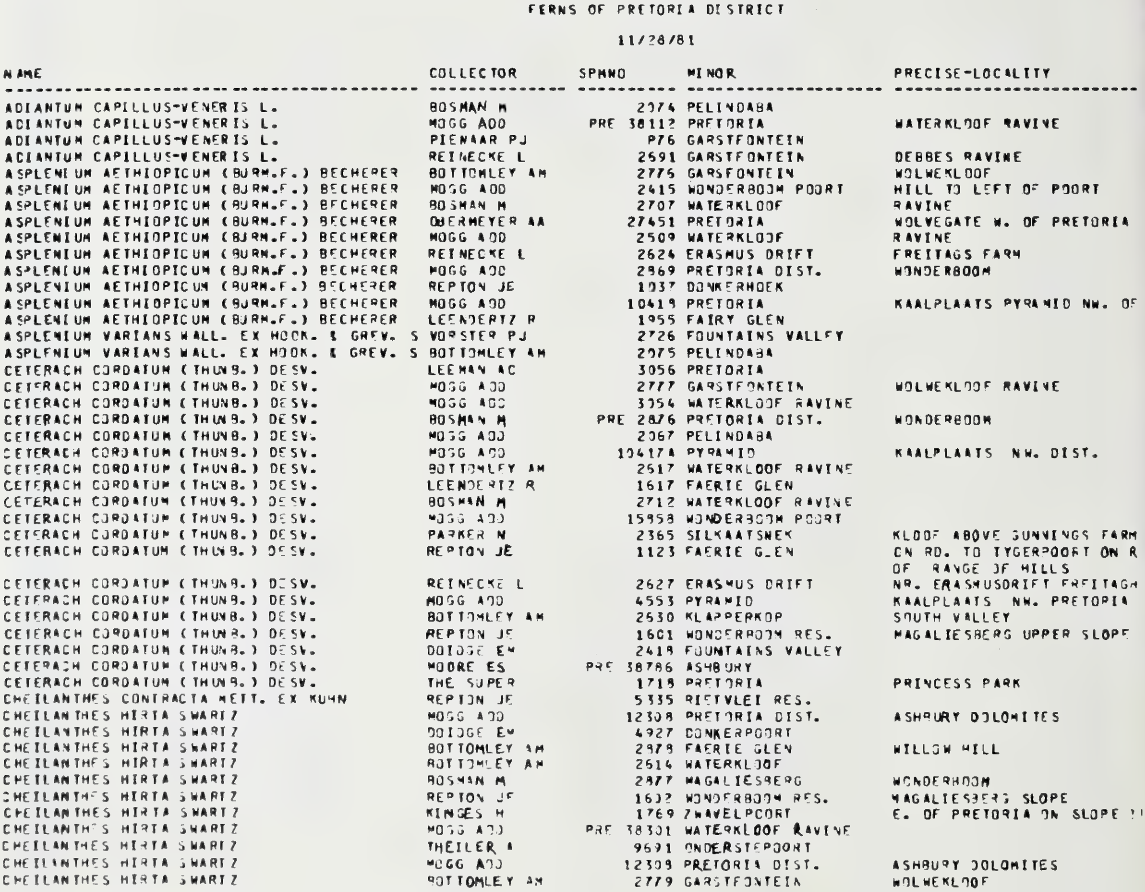
FIG. 9.—'Shelf list' of species in a genus.



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                                                      FERNS OF PRETORIA DISTRICT

                                                                11/28/81

NAME                                        COLLECTOR      SPMNO      MINOR                PRECISE-LOCALITY
------------------------------------------- -------------- ---------- -------------------- -------------------------
ADIANTUM CAPILLUS-VENERIS L.                BOSMAN M             2074 PELINDABA
ADIANTUM CAPILLUS-VENERIS L.                MOGG AOD        PRE 38112 PRETORIA             WATERKLOOF RAVINE
ADIANTUM CAPILLUS-VENERIS L.                PIENAAR PJ            P76 GARSTFONTEIN
ADIANTUM CAPILLUS-VENERIS L.                REINECKE L           2591 GARSTFONTEIN         DEBBES RAVINE
ASPLENIUM AETHIOPICUM (BURM.F.) BECHERER    BOTTOMLEY AM         2776 GARSFONTEIN          WOLWEKLOOF
ASPLENIUM AETHIOPICUM (BURM.F.) BECHERER    MOGG AOD             2415 WONDERBOOM POORT     HILL TO LEFT OF POORT
ASPLENIUM AETHIOPICUM (BURM.F.) BECHERER    BOSMAN M             2707 WATERKLOOF           RAVINE
ASPLENIUM AETHIOPICUM (BURM.F.) BECHERER    OBERMEYER AA        27451 PRETORIA             WOLVEGATE W. OF PRETORIA
ASPLENIUM AETHIOPICUM (BURM.F.) BECHERER    MOGG AOD             2509 WATERKLOOF           RAVINE
ASPLENIUM AETHIOPICUM (BURM.F.) BECHERER    REINECKE L           2624 ERASMUS DRIFT        FREITAGS FARM
ASPLENIUM AETHIOPICUM (BURM.F.) BECHERER    MOGG AOD             2969 PRETORIA DIST.       WONDERBOOM
ASPLENIUM AETHIOPICUM (BURM.F.) BECHERER    REPTON JE            1037 DONKERHOEK
ASPLENIUM AETHIOPICUM (BURM.F.) BECHERER    MOGG AOD            10419 PRETORIA             KAALPLAATS PYRAMID NW. OF
ASPLENIUM AETHIOPICUM (BURM.F.) BECHERER    LEENDERTZ R          1955 FAIRY GLEN
ASPLENIUM VARIANS WALL. EX HOOK. & GREV. S  VORSTER PJ           2726 FOUNTAINS VALLEY
ASPLENIUM VARIANS WALL. EX HOOK. & GREV. S  BOTTOMLEY AM         2975 PELINDABA
CETERACH CORDATUM (THUNB.) DESV.            LEEMAN AC            3056 PRETORIA
CETERACH CORDATUM (THUNB.) DESV.            MOGG AOD             2777 GARSTFONTEIN         WOLWEKLOOF RAVINE
CETERACH CORDATUM (THUNB.) DESV.            MOGG AOD             3054 WATERKLOOF RAVINE
CETERACH CORDATUM (THUNB.) DESV.            BOSMAN M         PRE 2876 PRETORIA DIST.       WONDERBOOM
CETERACH CORDATUM (THUNB.) DESV.            MOGG AOD             2067 PELINDABA
CETERACH CORDATUM (THUNB.) DESV.            MOGG AOD           104174 PYRAMID              KAALPLAATS  NW. DIST.
CETERACH CORDATUM (THUNB.) DESV.            BOTTOMLEY AM         2517 WATERKLOOF RAVINE
CETERACH CORDATUM (THUNB.) DESV.            LEENDERTZ R          1617 FAERIE GLEN
CETERACH CORDATUM (THUNB.) DESV.            BOSMAN M             2712 WATERKLOOF RAVINE
CETERACH CORDATUM (THUNB.) DESV.            MOGG AOD            15958 WONDERBOOM POORT
CETERACH CORDATUM (THUNB.) DESV.            PARKER N             2365 SILKAATSNEK          KLOOF ABOVE GUNNINGS FARM
CETERACH CORDATUM (THUNB.) DESV.            REPTON JE            1123 FAERIE GLEN          ON RD. TO TYGERPOORT ON R
                                                                                           OF  RANGE OF HILLS
CETERACH CORDATUM (THUNB.) DESV.            REINECKE L           2627 ERASMUS DRIFT        NR. ERASMUSDRIFT FREITAGH
CETERACH CORDATUM (THUNB.) DESV.            MOGG AOD             4553 PYRAMID              KAALPLAATS  NW. PRETORIA
CETERACH CORDATUM (THUNB.) DESV.            BOTTOMLEY AM         2530 KLAPPERKOP           SOUTH VALLEY
CETERACH CORDATUM (THUNB.) DESV.            REPTON JE            1601 WONDERBOOM RES.      MAGALIESBERG UPPER SLOPE
CETERACH CORDATUM (THUNB.) DESV.            DOIDGE EM            2419 FOUNTAINS VALLEY
CETERACH CORDATUM (THUNB.) DESV.            MOORE ES        PRE 38786 ASHBURY
CETERACH CORDATUM (THUNB.) DESV.            THE SUPER            1719 PRETORIA             PRINCESS PARK
CHEILANTHES CONTRACTA METT. EX KUHN         REPTON JE            5335 RIETVLEI RES.
CHEILANTHES HIRTA SWARTZ                    MOGG AOD            12308 PRETORIA DIST.       ASHBURY DOLOMITES
CHEILANTHES HIRTA SWARTZ                    DOIDGE EM            4927 DONKERPOORT
CHEILANTHES HIRTA SWARTZ                    BOTTOMLEY AM         2978 FAERIE GLEN          WILLOW HILL
CHEILANTHES HIRTA SWARTZ                    BOTTOMLEY AM         2614 WATERKLOOF
CHEILANTHES HIRTA SWARTZ                    BOSMAN M             2877 MAGALIESBERG         WONDERBOOM
CHEILANTHES HIRTA SWARTZ                    REPTON JE            1602 WONDERBOOM RES.      MAGALIESBERG SLOPE
CHEILANTHES HIRTA SWARTZ                    KINGES H             1769 ZWAVELPOORT          E. OF PRETORIA ON SLOPE
CHEILANTHES HIRTA SWARTZ                    MOGG AOD        PRE 38301 WATERKLOOF RAVINE
CHEILANTHES HIRTA SWARTZ                    THEILER A            9691 ONDERSTEPOORT
CHEILANTHES HIRTA SWARTZ                    MOGG AOD            12309 PRETORIA DIST.       ASHBURY DOLOMITES
CHEILANTHES HIRTA SWARTZ                    BOTTOMLEY AM         2779 GARSTFONTEIN         WOLWEKLOOF
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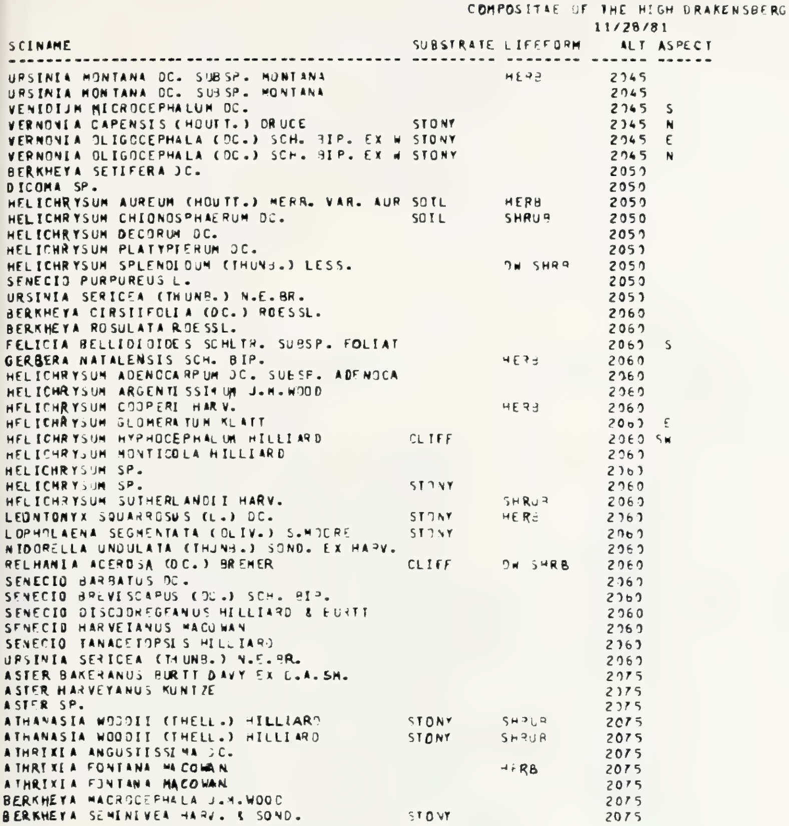
FIG. 10.—Specimens listed for a local flora.



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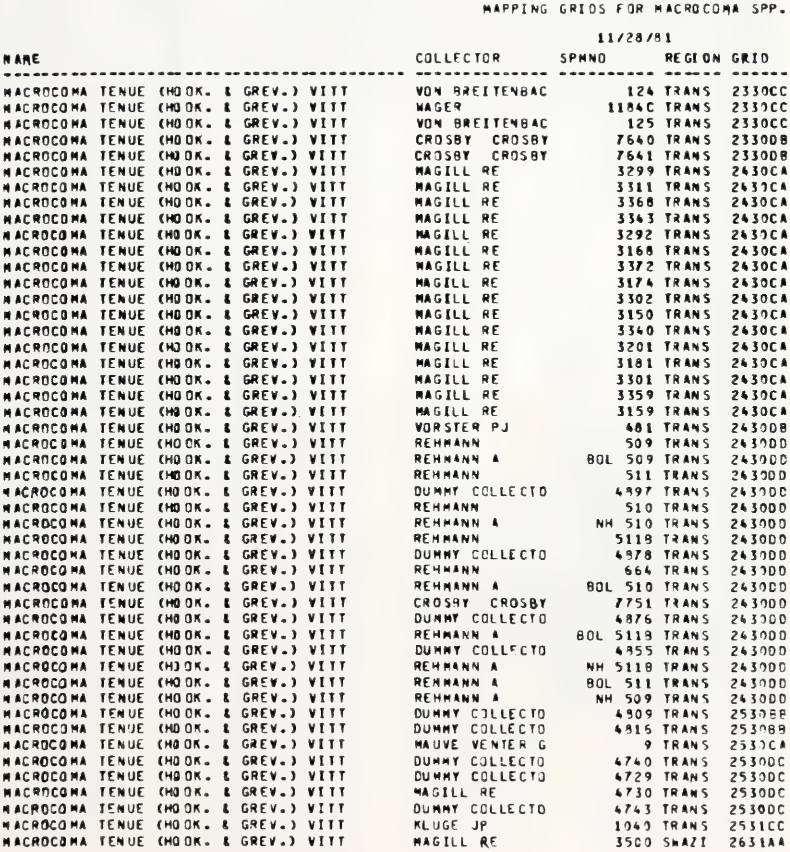
                                                          COMPOSITAE OF THE HIGH DRAKENSBERG
                                                                      11/28/81
SCINAME                                   SUBSTRATE LIFEFORM    ALT ASPECT
----------------------------------------- --------- -------- ------ ------
URSINIA MONTANA DC. SUBSP. MONTANA                  HERB       2045
URSINIA MONTANA DC. SUBSP. MONTANA                             2045
VENIDIUM MICROCEPHALUM DC.                                     2045  S
VERNONIA CAPENSIS (HOUTT.) DRUCE          STONY                2045  N
VERNONIA OLIGOCEPHALA (DC.) SCH. BIP. EX W STONY               2045  E
VERNONIA OLIGOCEPHALA (DC.) SCH. BIP. EX W STONY               2045  N
BERKHEYA SETIFERA DC.                                          2050
DICOMA SP.                                                     2050
HELICHRYSUM AUREUM (HOUTT.) MERR. VAR. AUR SOIL     HERB       2050
HELICHRYSUM CHIONOSPHAERUM DC.            SOIL      SHRUB      2050
HELICHRYSUM DECORUM DC.                                        2050
HELICHRYSUM PLATYPTERUM DC.                                    2050
HELICHRYSUM SPLENDIDUM (THUNB.) LESS.               DW SHRB    2050
SENECIO PURPUREUS L.                                           2050
URSINIA SERICEA (THUNB.) N.E.BR.                               2050
BERKHEYA CIRSIIFOLIA (DC.) ROESSL.                             2060
BERKHEYA ROSULATA ROESSL.                                      2060
FELICIA BELLIDIOIDES SCHLTR. SUBSP. FOLIAT                     2060  S
GERBERA NATALENSIS SCH. BIP.                        HERB       2060
HELICHRYSUM ADENOCARPUM DC. SUBSP. ADENOCA                     2060
HELICHRYSUM ARGENTISSIMUM J.M.WOOD                             2060
HELICHRYSUM COOPERI HARV.                           HERB       2060
HELICHRYSUM GLOMERATUM KLATT                                   2060  E
HELICHRYSUM HYPHOCEPHALUM HILLIARD        CLIFF                2060 SW
HELICHRYSUM MONTICOLA HILLIARD                                 2060
HELICHRYSUM SP.                                                2060
HELICHRYSUM SP.                           STONY                2060
HELICHRYSUM SUTHERLANDII HARV.                      SHRUB      2060
LEONTONYX SQUARROSUS (L.) DC.             STONY     HERB       2060
LOPHOLAENA SEGMENTATA (OLIV.) S.MOORE     STONY                2060
NIDORELLA UNDULATA (THUNB.) SOND. EX HARV.                     2060
RELHANIA ACEROSA (DC.) BREMER             CLIFF     DW SHRB    2060
SENECIO BARBATUS DC.                                           2060
SENECIO BREVISCAPUS (DC.) SCH. BIP.                            2060
SENECIO DISCODREGEANUS HILLIARD & BURTT                        2060
SENECIO HARVEIANUS MACOWAN                                     2060
SENECIO TANACETOPSIS HILLIARD                                  2060
URSINIA SERICEA (THUNB.) N.E.BR.                               2060
ASTER BAKERANUS BURTT DAVY EX C.A.SM.                          2075
ASTER HARVEYANUS KUNTZE                                        2075
ASTER SP.                                                      2075
ATHANASIA WOODII (THELL.) HILLIARD        STONY     SHRUB      2075
ATHANASIA WOODII (THELL.) HILLIARD        STONY     SHRUB      2075
ATHRIXIA ANGUSTISSIMA DC.                                      2075
ATHRIXIA FONTANA MACOWAN                            HERB       2075
ATHRIXIA FONTANA MACOWAN                                       2075
BERKHEYA MACROCEPHALA J.M.WOOD                                 2075
BERKHEYA SEMINIVEA HARV. & SOND.          STONY                2075
```

FIG. 11.—Specimens in a taxon sorted by altitude.



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                                                                       MAPPING GRIDS FOR MACROCOMA SPP.

                                                                                 11/28/81
NAME                                     COLLECTOR       SPHNO      REGION GRID
---------------------------------------- --------------- ---------- ------ ------
MACROCOMA TENUE (HOOK. & GREV.) VITT     VON BREITENBAC         124 TRANS  2330CC
MACROCOMA TENUE (HOOK. & GREV.) VITT     WAGER                1184C TRANS  2330CC
MACROCOMA TENUE (HOOK. & GREV.) VITT     VON BREITENBAC         125 TRANS  2330CC
MACROCOMA TENUE (HOOK. & GREV.) VITT     CROSBY  CROSBY        7640 TRANS  2330DB
MACROCOMA TENUE (HOOK. & GREV.) VITT     CROSBY  CROSBY        7641 TRANS  2330DB
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3299 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3311 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3368 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3343 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3292 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3168 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3372 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3174 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3302 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3150 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3340 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3201 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3181 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3301 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3359 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3159 TRANS  2430CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     VORSTER PJ             481 TRANS  2430DB
MACROCOMA TENUE (HOOK. & GREV.) VITT     REHMANN                509 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     REHMANN A          BOL 509 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     REHMANN                511 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     DUMMY COLLECTO        4897 TRANS  2430DC
MACROCOMA TENUE (HOOK. & GREV.) VITT     REHMANN                510 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     REHMANN A           NH 510 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     REHMANN               5118 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     DUMMY COLLECTO        4878 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     REHMANN                664 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     REHMANN A          BOL 510 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     CROSBY  CROSBY        7751 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     DUMMY COLLECTO        4876 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     REHMANN A         BOL 5118 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     DUMMY COLLECTO        4855 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     REHMANN A          NH 5118 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     REHMANN A          BOL 511 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     REHMANN A           NH 509 TRANS  2430DD
MACROCOMA TENUE (HOOK. & GREV.) VITT     DUMMY COLLECTO        4909 TRANS  2530BB
MACROCOMA TENUE (HOOK. & GREV.) VITT     DUMMY COLLECTO        4815 TRANS  2530BB
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAUVE VENTER G           9 TRANS  2530CA
MACROCOMA TENUE (HOOK. & GREV.) VITT     DUMMY COLLECTO        4740 TRANS  2530DC
MACROCOMA TENUE (HOOK. & GREV.) VITT     DUMMY COLLECTO        4729 TRANS  2530DC
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             4730 TRANS  2530DC
MACROCOMA TENUE (HOOK. & GREV.) VITT     DUMMY COLLECTO        4743 TRANS  2530DC
MACROCOMA TENUE (HOOK. & GREV.) VITT     KLUGE JP              1040 TRANS  2531CC
MACROCOMA TENUE (HOOK. & GREV.) VITT     MAGILL RE             3500 SWAZI  2631AA
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FIG. 12.—Specimens sorted by grid reference, for mapping.

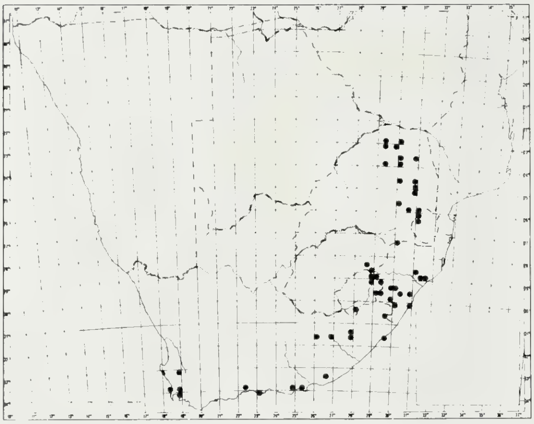


FIG. 13.—Distribution map prepared by hand from specimens sorted by grid reference.

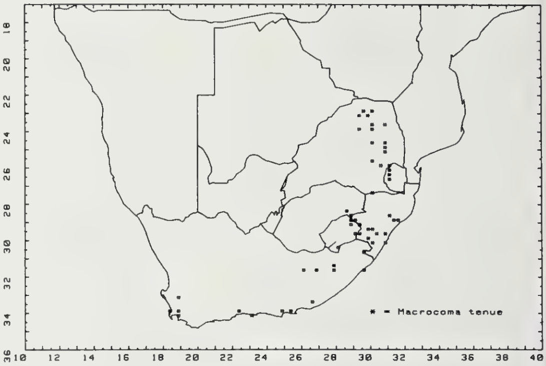
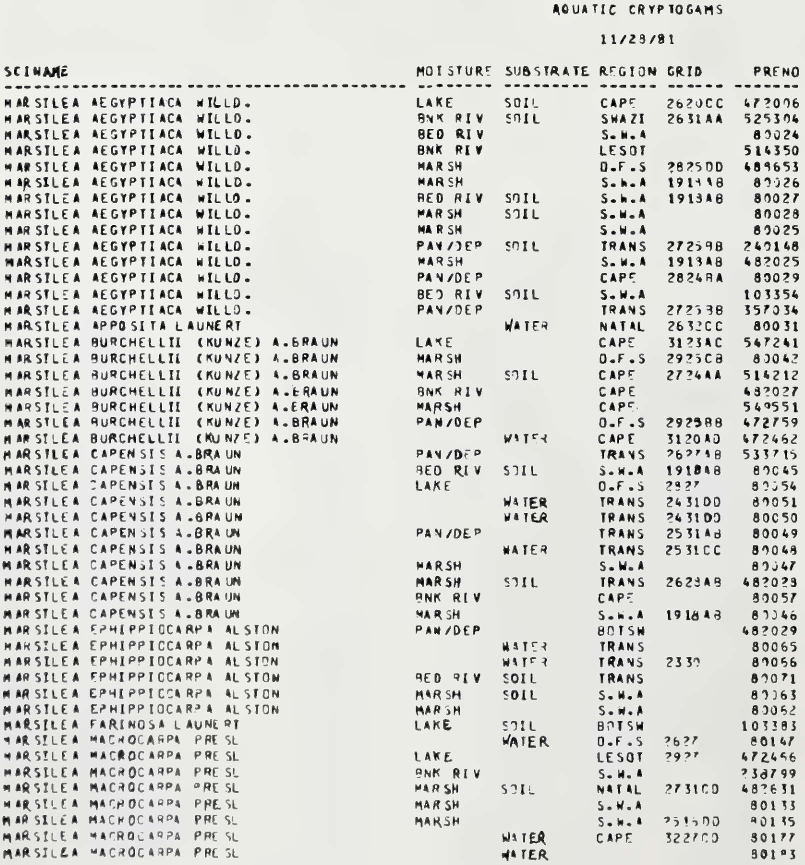


FIG. 14.—Distribution map prepared by Hewlett Packard desktop computer from specimens sorted by grid reference.



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                                                     AQUATIC CRYPTOGAMS

                                                          11/28/81

SCINAME                                               MOISTURE SUBSTRATE REGION GRID     PRENO
----------------------------------------------------  -------- --------- ------ ------ -------
MARSILEA AEGYPTIACA WILLD.                            LAKE     SOIL      CAPE   2620CC  472006
MARSILEA AEGYPTIACA WILLD.                            BNK RIV  SOIL      SWAZI  2631AA  525304
MARSILEA AEGYPTIACA WILLD.                            BED RIV            S.W.A           80024
MARSILEA AEGYPTIACA WILLD.                            BNK RIV            LESOT          514350
MARSILEA AEGYPTIACA WILLD.                            MARSH              O.F.S  2825DD  489653
MARSILEA AEGYPTIACA WILLD.                            MARSH              S.W.A  1913AB   80026
MARSILEA AEGYPTIACA WILLD.                            BED RIV  SOIL      S.W.A  1913AB   80027
MARSILEA AEGYPTIACA WILLD.                            MARSH    SOIL      S.W.A           80028
MARSILEA AEGYPTIACA WILLD.                            MARSH              S.W.A           80025
MARSILEA AEGYPTIACA WILLD.                            PAN/DEP  SOIL      TRANS  2725BB  240148
MARSILEA AEGYPTIACA WILLD.                            MARSH              S.W.A  1913AB  482025
MARSILEA AEGYPTIACA WILLD.                            PAN/DEP            CAPE   2824BA   80029
MARSILEA AEGYPTIACA WILLD.                            BED RIV  SOIL      S.W.A          103354
MARSILEA AEGYPTIACA WILLD.                            PAN/DEP            TRANS  2725BB  357034
MARSILEA APPOSITA LAUNERT                                      WATER     NATAL  2632CC   80031
MARSILEA BURCHELLII (KUNZE) A.BRAUN                   LAKE               CAPE   3123AC  547241
MARSILEA BURCHELLII (KUNZE) A.BRAUN                   MARSH              O.F.S  2925CB   80042
MARSILEA BURCHELLII (KUNZE) A.BRAUN                   MARSH    SOIL      CAPE   2724AA  514212
MARSILEA BURCHELLII (KUNZE) A.BRAUN                   BNK RIV            CAPE           482027
MARSILEA BURCHELLII (KUNZE) A.BRAUN                   MARSH              CAPE           549551
MARSILEA BURCHELLII (KUNZE) A.BRAUN                   PAN/DEP            O.F.S  2925BB  472759
MARSILEA BURCHELLII (KUNZE) A.BRAUN                            WATER     CAPE   3120AD  472462
MARSILEA CAPENSIS A.BRAUN                             PAN/DEP            TRANS  2627AB  533715
MARSILEA CAPENSIS A.BRAUN                             BED RIV  SOIL      S.W.A  1918AB   80045
MARSILEA CAPENSIS A.BRAUN                             LAKE               O.F.S  2927     80054
MARSILEA CAPENSIS A.BRAUN                                      WATER     TRANS  2431DD   80051
MARSILEA CAPENSIS A.BRAUN                                      WATER     TRANS  2431DD   80050
MARSILEA CAPENSIS A.BRAUN                             PAN/DEP            TRANS  2531AB   80049
MARSILEA CAPENSIS A.BRAUN                                      WATER     TRANS  2531CC   80048
MARSILEA CAPENSIS A.BRAUN                             MARSH              S.W.A           80047
MARSILEA CAPENSIS A.BRAUN                             MARSH    SOIL      TRANS  2623AB  482023
MARSILEA CAPENSIS A.BRAUN                             BNK RIV            CAPE            80057
MARSILEA CAPENSIS A.BRAUN                             MARSH              S.W.A  1918AB   80046
MARSILEA EPHIPPIOCARPA ALSTON                         PAN/DEP            BOTSW          482029
MARSILEA EPHIPPIOCARPA ALSTON                                  WATER     TRANS           80065
MARSILEA EPHIPPIOCARPA ALSTON                                  WATER     TRANS  2330     80056
MARSILEA EPHIPPIOCARPA ALSTON                         BED RIV  SOIL      TRANS           80071
MARSILEA EPHIPPIOCARPA ALSTON                         MARSH    SOIL      S.W.A           80063
MARSILEA EPHIPPIOCARPA ALSTON                         MARSH              S.W.A           80062
MARSILEA FARINOSA LAUNERT                             LAKE     SOIL      BOTSW          103383
MARSILEA MACROCARPA PRESL                                      WATER     O.F.S  2627     80147
MARSILEA MACROCARPA PRESL                             LAKE               LESOT  2927    472456
MARSILEA MACROCARPA PRESL                             BNK RIV            S.W.A          238799
MARSILEA MACROCARPA PRESL                             MARSH    SOIL      NATAL  2731CD  482631
MARSILEA MACROCARPA PRESL                             MARSH              S.W.A           80133
MARSILEA MACROCARPA PRESL                             MARSH              S.W.A  2515DD   80135
MARSILEA MACROCARPA PRESL                                      WATER     CAPE   3227CD   80177
MARSILEA MACROCARPA PRESL                                      WATER                     80193
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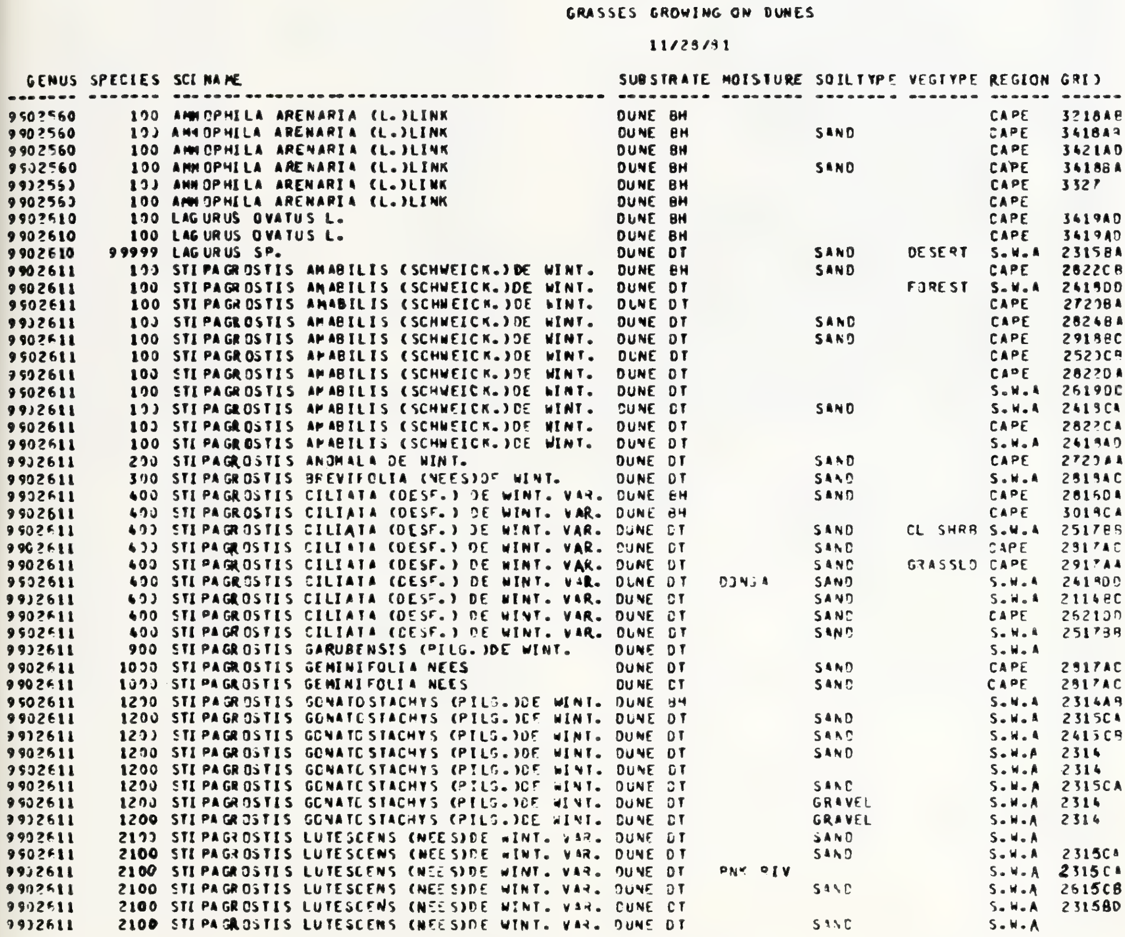
FIG. 15.—Example of a taxon sorted by life form and moisture regime.



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                                                  GRASSES GROWING ON DUNES

                                                          11/28/81

  GENUS SPECIES SCI NAME                                   SUBSTRATE MOISTURE SOILTYPE VEGTYPE REGION GRID
------- ------- ------------------------------------------ --------- -------- -------- ------- ------ ------
9902560     100 AMMOPHILA ARENARIA (L.)LINK                DUNE BH                             CAPE   3218AB
9902560     100 AMMOPHILA ARENARIA (L.)LINK                DUNE BH            SAND             CAPE   3418AB
9902560     100 AMMOPHILA ARENARIA (L.)LINK                DUNE BH                             CAPE   3421AD
9902560     100 AMMOPHILA ARENARIA (L.)LINK                DUNE BH            SAND             CAPE   3418BA
9902560     100 AMMOPHILA ARENARIA (L.)LINK                DUNE BH                             CAPE   3327
9902560     100 AMMOPHILA ARENARIA (L.)LINK                DUNE BH                             CAPE
9902610     100 LAGURUS OVATUS L.                          DUNE BH                             CAPE   3419AD
9902610     100 LAGURUS OVATUS L.                          DUNE BH                             CAPE   3419AD
9902610   99999 LAGURUS SP.                                DUNE DT            SAND     DESERT  S.W.A  2315BA
9902611     100 STIPAGROSTIS AMABILIS (SCHWEICK.)DE WINT.  DUNE BH            SAND             CAPE   2822CB
9902611     100 STIPAGROSTIS AMABILIS (SCHWEICK.)DE WINT.  DUNE DT                     FOREST  S.W.A  2419DD
9902611     100 STIPAGROSTIS AMABILIS (SCHWEICK.)DE WINT.  DUNE DT                             CAPE   2720BA
9902611     100 STIPAGROSTIS AMABILIS (SCHWEICK.)DE WINT.  DUNE DT            SAND             CAPE   2824BA
9902611     100 STIPAGROSTIS AMABILIS (SCHWEICK.)DE WINT.  DUNE DT            SAND             CAPE   2918BC
9902611     100 STIPAGROSTIS AMABILIS (SCHWEICK.)DE WINT.  DUNE DT                             CAPE   2520CB
9902611     100 STIPAGROSTIS AMABILIS (SCHWEICK.)DE WINT.  DUNE DT                             CAPE   2822DA
9902611     100 STIPAGROSTIS AMABILIS (SCHWEICK.)DE WINT.  DUNE DT                             S.W.A  2619DC
9902611     100 STIPAGROSTIS AMABILIS (SCHWEICK.)DE WINT.  DUNE DT            SAND             S.W.A  2419CA
9902611     100 STIPAGROSTIS AMABILIS (SCHWEICK.)DE WINT.  DUNE DT                             CAPE   2822CA
9902611     100 STIPAGROSTIS AMABILIS (SCHWEICK.)DE WINT.  DUNE DT                             S.W.A  2419AD
9902611     200 STIPAGROSTIS ANOMALA DE WINT.              DUNE DT            SAND             CAPE   2720AA
9902611     300 STIPAGROSTIS BREVIFOLIA (NEES)DE WINT.     DUNE DT            SAND             S.W.A  2819AC
9902611     400 STIPAGROSTIS CILIATA (DESF.) DE WINT. VAR. DUNE BH            SAND             CAPE   2816DA
9902611     400 STIPAGROSTIS CILIATA (DESF.) DE WINT. VAR. DUNE BH                             CAPE   3019CA
9902611     400 STIPAGROSTIS CILIATA (DESF.) DE WINT. VAR. DUNE DT            SAND     CL SHRB S.W.A  2517BB
9902611     400 STIPAGROSTIS CILIATA (DESF.) DE WINT. VAR. DUNE DT            SAND             CAPE   2917AC
9902611     400 STIPAGROSTIS CILIATA (DESF.) DE WINT. VAR. DUNE DT            SAND     GRASSLD CAPE   2917AA
9902611     400 STIPAGROSTIS CILIATA (DESF.) DE WINT. VAR. DUNE DT   DONGA    SAND             S.W.A  2419DD
9902611     400 STIPAGROSTIS CILIATA (DESF.) DE WINT. VAR. DUNE DT            SAND             S.W.A  2114BC
9902611     400 STIPAGROSTIS CILIATA (DESF.) DE WINT. VAR. DUNE DT            SAND             CAPE   2621DD
9902611     400 STIPAGROSTIS CILIATA (DESF.) DE WINT. VAR. DUNE DT            SAND             S.W.A  2517BB
9902611     900 STIPAGROSTIS GARUBENSIS (PILG.)DE WINT.    DUNE DT                             S.W.A
9902611    1000 STIPAGROSTIS GEMINIFOLIA NEES              DUNE DT            SAND             CAPE   2917AC
9902611    1000 STIPAGROSTIS GEMINIFOLIA NEES              DUNE DT            SAND             CAPE   2817AC
9902611    1200 STIPAGROSTIS GONATOSTACHYS (PILG.)DE WINT. DUNE BH                             S.W.A  2314AB
9902611    1200 STIPAGROSTIS GONATOSTACHYS (PILG.)DE WINT. DUNE DT            SAND             S.W.A  2315CA
9902611    1200 STIPAGROSTIS GONATOSTACHYS (PILG.)DE WINT. DUNE DT            SAND             S.W.A  2415CB
9902611    1200 STIPAGROSTIS GONATOSTACHYS (PILG.)DE WINT. DUNE DT            SAND             S.W.A  2314
9902611    1200 STIPAGROSTIS GONATOSTACHYS (PILG.)DE WINT. DUNE DT                             S.W.A  2314
9902611    1200 STIPAGROSTIS GONATOSTACHYS (PILG.)DE WINT. DUNE DT            SAND             S.W.A  2315CA
9902611    1200 STIPAGROSTIS GONATOSTACHYS (PILG.)DE WINT. DUNE DT            GRAVEL           S.W.A  2314
9902611    1200 STIPAGROSTIS GONATOSTACHYS (PILG.)DE WINT. DUNE DT            GRAVEL           S.W.A  2314
9902611    2100 STIPAGROSTIS LUTESCENS (NEES)DE WINT. VAR. DUNE DT            SAND             S.W.A
9902611    2100 STIPAGROSTIS LUTESCENS (NEES)DE WINT. VAR. DUNE DT            SAND             S.W.A  2315CA
9902611    2100 STIPAGROSTIS LUTESCENS (NEES)DE WINT. VAR. DUNE DT   PNK RIV                   S.W.A  2315CA
9902611    2100 STIPAGROSTIS LUTESCENS (NEES)DE WINT. VAR. DUNE DT            SAND             S.W.A  2615CB
9902611    2100 STIPAGROSTIS LUTESCENS (NEES)DE WINT. VAR. DUNE DT                             S.W.A  2315BD
9902611    2100 STIPAGROSTIS LUTESCENS (NEES)DE WINT. VAR. DUNE DT            SAND             S.W.A
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FIG. 16.—Example of a taxon sorted by habitat.

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                                                           FOREST CLIMBERS

                                                              11/28/81

  GENUS SPECIES SCI NAME                                   GRID   MAJR                 MINR
------- ------- ------------------------------------------ ------ -------------------- --------------------
8309000     500 TRICALYSIA CAPENSIS (MEISN.) SIM           2831CD ESHOWE DIST          DHLINZA FOR
8309000     600 TRICALYSIA JUNODII (SCHINZ) BRENAN VAR. JU 2731AA                      MAKANES
8352000     400 CANTHIUM GUEINZII SOND.                           MAPUMULO DIST        THRINGS POST.
8352000     400 CANTHIUM GUEINZII SOND.                    2631AC                      MBABANE
8352000     400 CANTHIUM GUEINZII SOND.                                                MARIEPSKOP DIST.
8352000     400 CANTHIUM GUEINZII SOND.                    3129DA TRANSKEI             NTAFUFU
8352000     400 CANTHIUM GUEINZII SOND.                    2631AC                      MBABANE
8352000     400 CANTHIUM GUEINZII SOND.                    2931AD LOWER TUGELA DIST.   STANGER
8352000     400 CANTHIUM GUEINZII SOND.                    2430DB PILGRIMS REST DIST.  MARIEPSKOP
8352000     400 CANTHIUM GUEINZII SOND.                    3030CB PORT SHEPSTONE       ST. MICHAEL'S-ON-SEA
8352000     400 CANTHIUM GUEINZII SOND.                                                MTUNZINI DIST.
8352000     400 CANTHIUM GUEINZII SOND.                                                HLABISA DIST.
8352000     400 CANTHIUM GUEINZII SOND.                    2330CA EASTERN CAPE         DUIWELSKLOOF
8352000     400 CANTHIUM GUEINZII SOND.                    3030CB PORT SHEPSTONE       ST. MICHAEL'S-ON-SEA
8352000     400 CANTHIUM GUEINZII SOND.                    2531CD
8352000     400 CANTHIUM GUEINZII SOND.                                                NKANDLA DIST.
8352000     400 CANTHIUM GUEINZII SOND.                           MBABANE DIST.        UKUTULA FOR.
8352000     400 CANTHIUM GUEINZII SOND.                    2831CA NKANDLA DIST.        NKANDLA FOR.
8352000     400 CANTHIUM GUEINZII SOND.                                                MARIEPSKOP DIST.
8352000     500 CANTHIUM HUILLENSE HIERN                   2231CA KRUGER NAT. PARK     PUNDA MILIA
8352000     600 CANTHIUM INERME (L.F.) KUNTZE                                          INANDA DIST.
8352000     600 CANTHIUM INERME (L.F.) KUNTZE              2831AD                      LAKE ST. LUCIA
8352000     600 CANTHIUM INERME (L.F.) KUNTZE              2631DD                      MAPUTA
8352000    1100 CANTHIUM SETIFLORUM HIERN                         NDUMU GAME RES.      KHONDO SAND FOR
8352000    1100 CANTHIUM SETIFLORUM HIERN                  2731CB
8352000   99999 CANTHIUM SP.                               2930CE PIETERMARITZBURG DIS WORLDS VIEW
8333000    1500 PAVETTA DELAGOENSIS BREM.                  2731BC                      LAKE SIBAYI
8399000     100 PSYCHOTRIA CAPENSIS (ECKL.) VATKE                                      MAPUMULO DIST
8486000    1100 GALIUM SPURIUM L. SUBSP. AFRICANUM VERDC.         HEIDELBERG DIST.     GROOTVADERSBOSCH FOR
8486000    1100 GALIUM SPURIUM L. SUBSP. AFRICANUM VERDC.  2828BC BETHLEHEM DIST.      GOLDEN GATE HIGHLAND
8486000    1270 GALIUM THUNBERGIANUM ECKL. & ZEYH. VAR. TH 2828DD                      MONT AUX SOURCES
8486000   99999 GALIUM SP.                                        ZUURBERG             ALFRED DIST
8489000     100 RUBIA CORDIFOLIA L.                                                    NEW HANOVER DIST.
8489000     100 RUBIA CORDIFOLIA L.                        2731DA                      SORDWANA BAY
8489000     100 RUBIA CORDIFOLIA L.                        2930CC                      KEEROM
8489000     100 RUBIA CORDIFOLIA L.                        2831CD                      ESHOWE
8489000     100 RUBIA CORDIFOLIA L.                        2832AA HLABISA              HLUHLUWE GAME RES.
8489000     100 RUBIA CORDIFOLIA L.                        2832AA HLABISA DIST.        HLUHLUWE GAME RES.
8489000     300 RUBIA PETIOLARIS DC.                       2531CC                      BARBERTON
8489000     300 RUBIA PETIOLARIS DC.                              AMATOLA MTS          VICTORIA EAST
8546000     700 SCABIOSA DRAKENSBERGENSIS B.L.BURTT        2828DB BERGVILLE DIST.      DRAKENSBERG NAT PARK
8564000     100 ZEHNERIA MARLOTHII (COGN.) R. & A.FERNANDE        NORTHERN DIST.       MUTSOI
8564000     200 ZEHNERIA PARVIFOLIA (COGN.) J.H.ROSS       2832AA HLABISA DIST.        HLUHLUWE GAME RES.
8564000     200 ZEHNERIA PARVIFOLIA (COGN.) J.H.ROSS       2831CC ZULULAND             UMHLATUZI LAKE
8564000     200 ZEHNERIA PARVIFOLIA (COGN.) J.H.ROSS       2632DC INGWAVUMA DIST.      MAPUTA
8564000     300 ZEHNERIA SCABRA (L.F.) SOND.               2230CD SIBASA DIST.         TATE VONDO FOR. RES.
8564000     300 ZEHNERIA SCABRA (L.F.) SOND.               2831DC MTUNZINI DIST.       NGOYE FOR. RES.
8564000     300 ZEHNERIA SCABRA (L.F.) SOND.               2430DD GRASKOP              KOWYNSPAS
```

FIG. 17.—Example of specimens sorted for two habitat factors.

```
                                                 DWARF SHRUBS OF FYNBOS LIMESTONE SOILS

                                                              11/28/81

  GENUS SPECIES SCI NAME                                   GRID   MAJR                 MINR
------- ------- ------------------------------------------ ------ -------------------- --------------------
6503000     200 CHIRONIA BACCIFERA L.                                                  BREDASDORP DIV.
6237000   16000 ERICA CURTOPHYLLA GUTH. & BOL.             3421AC                      RIVERSDALE
6237000   16000 ERICA CURTOPHYLLA GUTH. & BOL.             3421AC                      RIVERSDALE
6237000   53900 ERICA PULCHELLA HOUTT. VAR. PULCHELLA      3420BD WELKHOUT KRAAL       RONDEKOP
6237000   56700 ERICA RUBIGINOSA DULFER VAR. RUBIGINOSA    3420CA                      BREDASDORP
5436000    1000 STRUTHIOLA DODECANDRA (L.) DRUCE           3419DA                      HAGELKRAAL RIVER
5436000    1000 STRUTHIOLA DODECANDRA (L.) DRUCE           3419DA SOUTH-WESTERN CAPE   HAELKRAAL RIVER AREA
```

FIG. 18.—Example of specimens sorted by three habitat factors.

```
FLOWERING PHENOLOGY OF THEMEDA TRIANDRA

                 11/28/81

NO REGION      ALT FLOWER FRUIT GRID
-- ------ ------ ------ ----- ------
 1 TRANS    -999      3     3 2528CD
 1 TRANS    -999      3     3 2528CD
 1 TRANS    -999      3     3 2529CB
 1 TRANS    -999      3     3 2530DB
 1 TRANS    1300      3     3 2530DD
 1 TRANS    1300      3     3 2530DD
 1 TRANS    -999      3     3 2531CC
 1 TRANS    1370      3     3 2625AA
 1 TRANS    -999      3     3 2627AC
 1 TRANS    -999      3     3 2627CA
 1 TRANS    -999      3     3 2628AA
 1 TRANS    1800      3     3 2628AA
 1 TRANS    -999      3     3 2628AA
 1 TRANS    -999      3     3 2628AA
 1 TRANS    -999      3     3 2629BD
 1 TRANS    -999      3     3 2629CD
 1 TRANS    -999      3     3 2629CD
 1 TRANS    -999      3     3 2629DB
 1 O.F.S    -999      3     3 2629DB
 1 TRANS    -999      3     3 2629DB
 1 SWAZI    -999      3     3 2631BB
 1 SWAZI     275      2     3 2631BD
 1 S.W.A    -999      3     3 2719BD
 1 TRANS    -999      3     3 2725CC
 1 TRANS    1214      3     3 2725DA
 1 TRANS    1370      3     3 2725AC
 1 O.F.S    -999      3     3 2725BC
 1 O.F.S    -999      3     3 2726CD
 1 O.F.S    -999      3     3 2725CD
 1 O.F.S    -999      3     3 2727BD
 1 O.F.S    -999      3     3 2727CC
 1 TRANS    -999      3     3 2730BA
 1 NATAL     667      3     3 2731CA
 1 NATAL    -999      3     3 2732DA
 1 CAPE     -999      3     3 2822DD
 1 TRANS    -999      3     3 2824CC
 1 TRANS    -999      3     3 2824CC
 1 TRANS    -999      3     3 2824CC
 1 TRANS    -999      3     3 2824CC
 1 TRANS    -999      3     3 2824CC
 1 TRANS    -999      3     3 2824CC
 1 O.F.S    1500      3     3 2827AB
 1 O.F.S    -999      3     3 2827DD
 1 O.F.S    1509      3     3 2827DD
 1 O.F.S    -999      3     3 2827DD
 1 O.F.S    1575      3     3 2828AD
 1 O.F.S    -999      3     3 2828BC
 1 O.F.S    1390      3     3 2828DA
```

FIG. 19.—Specimens in a species sorted by month of flowering.

or grasses growing on sand dunes (Fig. 16). The fields can also be used in combination for lists of forest climbers (Fig. 17), or dwarf shrubs of fynbos on calcrete (Fig. 18), for instance.

Phenological data are also available by selecting all flowering specimens of a taxon and printing the date of collection and other related information such as region, altitude or aspect (Fig. 19).

CONCLUSION

The new system, which will retain the name PRECIS (PRE Computerized Information System), has a smaller but more accessible data base contained in a single disk pack for on-line service. It is designed primarily to provide specimen data for taxonomic and floristic research, but some taxon-related specimen data can be extracted from the information recorded with the specimens.

From our reappraisal and modification of the original system we can make some statements that should apply to all data banks of this type.

1. The data bank should be kept as small as possible, preferably covering only a single information category, such as specimen related data.

2. Encoding and manipulation of data must be kept as simple as possible not only for the collector, but also to enable proper maintenance and updating of the data bank.

3. Rapid access to the data is essential for research and curation, preferably as an on-line service. This includes the necessity of modest expense for routine or essential queries, updating procedures and curatorial output.

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Phytogeography of the copper and cobalt flora of Upper Shaba (Zaïre), with emphasis on its endemism, origin and evolution mechanisms

F. P. MALAISSE*

ABSTRACT

Copper and cobalt ore deposits occur on at least a hundred outcrops scattered in the Shaban Copperbow, an area of 2 000 square kilometres, in the metallogenic Province of Southern Central Africa. With more than 200 species, this flora includes a large number (42) of endemic species of various degrees. Some species are known from only one site, many are located on neighbouring outcrops, others occur on all the ore deposits. Present migratory pathways have been traced for some species and are reported. The relative importance of palaeoendemism and neoendemism is discussed. The origin of these endemics, as well as that of other plants is to be found in several adjacent floras such as that of steppe-savannas developed on more or less poorly aerated soils (Kalahari sands or dambos overlaying laterite), dwarf vegetation on siliceous cellular rocks and miombo woodlands on poor hydromorphic soils. Examples are given for each vegetation type. Systematic details, leaf anatomy and phytogeochemistry data support these hypotheses, which are illustrated for several closely related taxa.

RÉSUMÉ

Au moins cent gisements de cuivre et de cobalt existent dans l'Arc cuprifère shabien, un territoire de quelques 2 000 km^2 situé dans la Province métallogénique d'Afrique centrale méridionale. Avec une diversité spécifique qui excède 200 plantes, cette flore comprend un nombre important de taxa endémiques (42) de niveau varié. Certaines espèces sont connues d'une seule localité, un certain nombre de plantes sont situées sur des gisements voisins, d'autres encore s'observent sur toutes les anomalies métallifères. Les voies de migration actuelle ont été suivies pour certaines espèces et sont signalées. L'importance relative du paléoendémisme et du néoendémisme est discutée. L'origine de ces endémiques, aussi bien que l'origine des autres plantes observées est à rechercher parmi certaines flores voisines telles que celle des savanes steppiques développées sur des sols plus ou moins asphyxiants (sables du Kalahari ou dembos établis sur latérite), la végétation naine des roches siliceuses cellulaires et les forêts claires situées sur des sols à mauvaises conditions hydromorphiques. Des exemples sont donnés de l'apport de chacun de ces types de végétation. Des données systématiques, d'anatomie foliaire et phytogéochimiques renforcent ces hypothèses, qui sont illustrées pour plusieurs taxa voisins.

INTRODUCTION

Southern Central Africa is an important metallogenic Province, where many ore deposits occur, namely of copper, a metal with which cobalt is frequently associated (Fig. 1). The flora and the vegetation of these ore deposits have been the subject of many studies, not only in Shaba (Robyns, 1932; Duvigneaud, 1958, 1959; Duvigneaud & Timperman, 1959; Duvigneaud & Denaeyer-De Smet, 1960, 1963; Schmitz, 1963; Brooks, 1977; Brooks *et al.*, 1977, 1978; Malaisse & Grégoire, 1978; Malaisse *et al.*, 1978, 1979, 1982; Morrison *et al.*, 1979, 1981; Shewry *et al.*, 1979; De Plaen *et al.*, 1982; Malaisse & Brooks, 1982), but also in Zimbabwe (Jacobsen, 1967, 1968, 1970; Wild, 1968; Howard-Williams, 1970, 1971, 1972; Ernst, 1972) and in Zambia (Horscroft, 1961; Reilly, 1967, 1969, 1971; Drew & Reilly, 1972). Ernst (1974), Wild (1978) and Brooks *et al.* (1980) reviewed the present state of knowledge.

In Shaba, about 100 copper-cobalt deposits totalling some 20 km^2 are scattered in a 20 000 km^2 area of the Shaban Copperbow in south-east Zaïre (Morrison *et al.* 1981). These deposits support a distinct vegetation. Both endemic taxa and a great number of more widely distributed species can be distinguished within this flora, origin of which is mainly to be found in the surrounding vegetation types, of which the main types were noted by Duvigneaud (1958). However, preliminary lists permitting an appreciation of respective origins, are not yet available. Moreover, as far as endemism is concerned, both palaeoendemism (Wild, 1971; Wild & Bradshaw, 1977) as defined by Stebbins (1942) and neoendemism (Antonovics *et al.*, 1971) have been proposed, although the speciation mechanisms have never been precisely examined. The present study attempts to assemble data relating to this lack of knowledge.

ENDEMISM OF THE COPPER-COBALT FLORA OF UPPER SHABA

The number of endemic species of the copper-cobalt flora of Upper Shaba may be estimated at present at some 42 taxa. This number will undoubtedly change as a result of new systematic studies and further collecting. Revisions may reveal some taxa, until now considered as endemics, to be synonymous. For instance, Geerinck (1971), whose wider concept of the idea of species differs from the narrower view of Duvigneaud and Van Bockstal (Duvigneaud, 1959; Duvigneaud & Denaeyer-De Smet, 1963), reduces the number of *Gladiolus* occurring on copper soils to six, with only one endemic species, *Gladiolus robiliartianus* Duvign.

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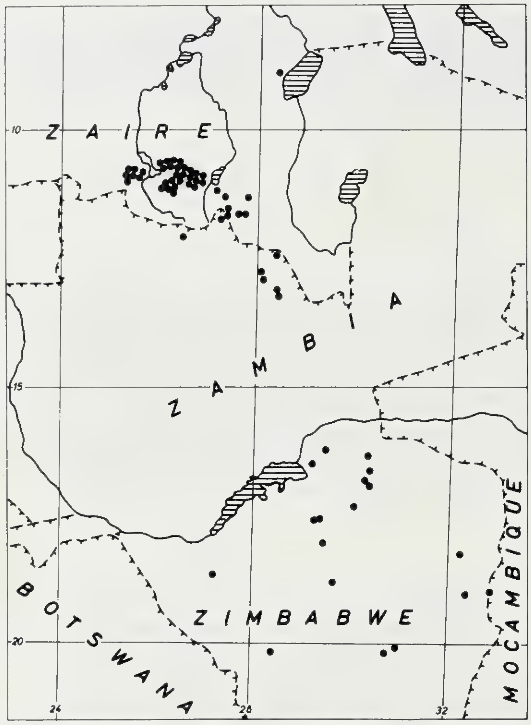

FIG. 1.— Copper (and cobalt) ore deposits in the south central African metallogenic Province.

According to him, several copper endemic taxa, namely *G. tshombeanus* Duvign. & Van Bockst., *G. peschianus* Duvign. & Van Bockst., *G. fungurumeensis* Duvign. & Van Bockst. and *G. duvigneaudii* Van Bockst. appear to be synonyms of species found outside copper soils. On the other hand, some species may be described in error, as was recently the case of *Batopedina pulvinellata* Robbrecht, or are still waiting to be described, such as the new *Monadenium* species (*Malaisse* 11515) that we have observed recently at Tilwezembe and Fungurume. The examination of recent gatherings may also modify some distributions. For instance, the presence of *Haumaniastrum katangense* (S. Moore) Duvign. & Plancke, outside copper outcrops in N.E. Zambia has recently been noted (Malaisse & Brooks, 1982); moreover, it has been established that this plant occurs on various man-made metalliferous locations, such as the sites of old precolonial furnaces for copper smelting (De Plaen *et al.*, 1982). This plant, considered for a long time as a 'copper flower', is no longer endemic to copper outcrops, even if it remains a very useful indicator of copper anomalies in Shaba. Nevertheless, these preliminary remarks permit certain deductions. Copper-cobalt flora endemism shows several aspects (Fig. 2). Besides plants occurring on all copper-cobalt ore deposits (*Ascolepis metallorum* Duvign. & G. Léonard, *Acalypha cupricola* Robyns) or those with an irregular distribution but widely present in the ensemble of about hundred deposits (*Pandiaka metallorum* Duvign. & Van Bockst., *Rendlia cupricola* Duvign.), endemic plants whose distribution is restricted to some neighbouring sites exist. There are even plants that are known from only one site, such as *Lindernia perennis* Duvign. and *Vigna dolomitica* Wilczek observed at Etoile Mine, *Sporobolus deschampsioides* Duvign. observed on Kamwali Hill, *Karina tayloriana* Boutique of Kasompi Mine, *Silene cobalticola* Duvign. & Plancke of Mindigi Mine, *Crotalaria françoisiana* Duvign. & Timp. on Mupine hillock and *Acalypha dikuluwensis* Duvign. & Dewit, *Eragrostis dikuluwensis* Duvign. & Jacobs, *Dissotis derriksiana* Duvign. and *Streptocarpus rhodesianus* S. Moore var. *perlanatus* Duvign., all endemics to the Dikuluwe Mine. The totally distinct vegetation of Dikuluwe and Mupine is now completely destroyed as a result of mining (annual copper production of Shaba has passed from 10 (1914) to 426 (1980) 10^3 metric tons). Examples of plants restricted to some neighbouring sites or to a part of the Shaban Copperbow are given in Fig. 2. For example, *Buchnera duvigneaudii* Malaisse* presents a distribution limited to the Kalongwe-Kasompi axis, *Becium peschianum* Duvign. & Plancke is found only on outcrops in the S.E. and *Haumaniastrum robertii* (Robyns) Duvign. & Plancke exists in the central and western part of the Copperbow, etc.

Endemic species, clearly separated from neighbouring taxa not present in Shaba, and which are moreover widely distributed on copper deposits. probably belong to paleoendemism, as is the case of *Ascolepis metallorum*, *Acalypha cupricola* and *Rendlia cupricola*. The first of these three species can still be found on the Kengere deposits, where it resists high zinc-lead concentrations (Duvigneaud & Denaeyer-De Smet, 1963) whereas *Rendlia cupricola,* has been observed outside the Shaban Copperbow at Dikulushi, on copper deposits in the vicinity of Lake Moero. We also noted its presence on anthropic metalliferous sites such as the alluvious soils polluted by waste water of the factory at Likasi, along the Panda River, an ecological niche occupied by *Pteris vittata* L. in the area surrounding Lubumbashi. Neoendemism, on the other hand, should be considered for plastic species, where intermediate forms may still be observed, notably mine ecotypes corresponding to the differentiation of 'small' species, generally having a limited distribution. *Silene cobalticola*, several species of *Becium*, *Haumaniastrum timpermanii* (Duvign. & Plancke) Duvign. & Plancke subsp. *kambovianum* (Duvign. & Plancke) Duvign. & Plancke, etc belong to this last category. In conclusion, the copper-cobalt endemics of Upper Shaba contain a large number of neoendemic species to which may be added a small number of palaeoendemics. This dual origin can be explained (1) by the age of copper-cobalt mineralization in Upper Shaba, which dates from late precambrian era and has therefore been in existence for more than 620 million years and (2) by the extreme climatic changes which

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* *Buchnera duvigneaudii* Malaisse, *nomen novum* : *Buchnera candida* Duvign. & Van Bockst. syn. nov., non *B. candida* S. Moore (holotype: *Duvigneaud* 3106 B2, other gathering: *Malaisse* 10794).

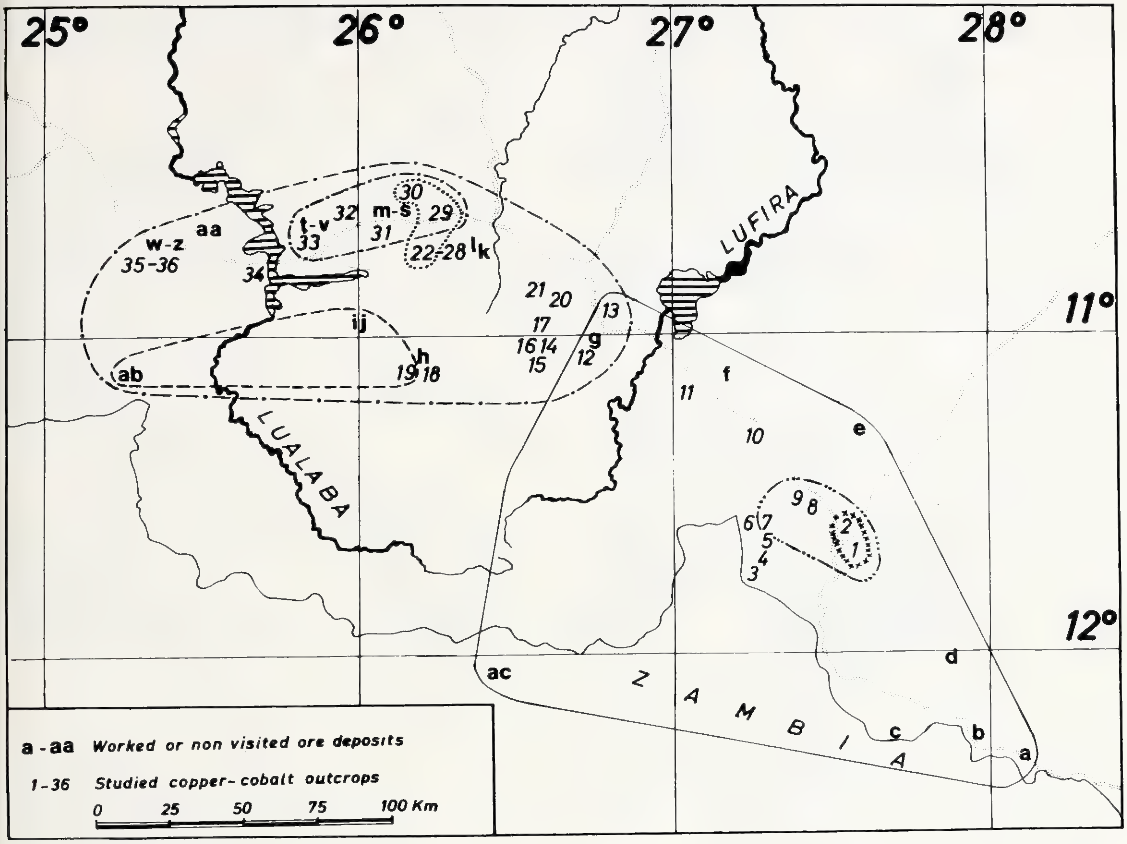

FIG. 2.— Endemism in the Upper-Shaban copper-cobalt flora. Ore deposits are: a, Kamikuba; b, Kinsenda; c, Musoshi; d, Kipapila; e, Lusevere; f, Kamwali; g, Likasi; h, Mirungwe; i, Kasompi; j, Menda; k, Kakanda; l, Kiwana; m, Kakavilondo; n, Tenke; o, Goma; p, Shimbidi, q, Kavifwafwaulu; r, Lumbele; s, Mwinansefu; t, Kasunki; u, Chitamba; v, Kakontolwa; w, Mupine; x, Kamoto; y, Musonoi; z, Kolwezi; aa, Ruwe; ab, Kalongwe; ac, Kansanshi; and 1, Etoile; 2, Ruashi; 3, Kipushi; 4, Kasombo; 5, Karavia; 6, Lupoto; 7, Kasonta; 8, Luiswishi; 9, Lukuni; 10, Sokoroshe; 11, Luishia; 12, Shituru; 13, Kamatanda; 14–16, Shinkolowe (principal, signal, borne 13); 17, Tantara; 18, Swambo; 19, Mindigi; 20, Kambove; 21, Sesa; 22, Kela; 23, Mupapala; 24, Lufomboshi; 25, Kankeru; 26, Disele; 27, Kahumbwe; 28, Luita; 29, Fungurume; 30, Kwatebala; 31, Kabwelunono; 32, Kalukundi; 33, Chabara; 34, Tilwezembe; 35, Dikuluwe; 36, Mashamba. Several endemic distributions are represented: ——— *Haumaniastrum katangense;* —— —— ● *Haumaniastrum robertii;* ×××××× *Faroa chalcophila;* —— ●●● —— *Becium peschianum;* ●●●●●●● *Buchnera rubriflora;* ● — ● — ● *Buchnera foliosa;* — — — — *Buchnera duvigneaudii. Ascolepis metallorum* is found on all the ore deposits, whereas some plants are restricted to one mine.

characterized the tertiary era and which therefore created numerous vacant ecological niches at the beginning of the quaternary. These may have favoured the differentiation of species little able to compete in normal conditions, such as *Haumaniastrum katangense*, which reveals a clear weakness to fungal attacks when copper is absent (Morrison *et al.*, 1979).

ORIGIN OF THE COPPER-COBALT FLORA OF UPPER SHABA

As far as is known at present, the copper-cobalt flora of Upper Shaba comprises some 220 taxa including 42 endemics. The origin of this flora is to be found in several vegetation types (Fig. 3). According to Duvigneaud (1958), these plants are derived from four main sources: steppe-savannas on sandy high plateaux (dilungus) (A), seasonally inundated steppe-savannas overlying laterite (dambos) (E), woodlands on yellow compact soils (F) and formations on non-mineralized rocky outcrops (I). However we have also noted other ecological groups, namely grassland plants not subjected to seasonal flooding (B), grassland plants with a wide ecological amplitude (C), plants occurring on derived savannas (D), ruderal species (G) and basi or (and) xerophilous plants (H). Malaisse & Grégoire (1978) listed some ruderal plants occurring on copper mines and Malaisse *et al.* (1983) listed the contribution of the flora of high plateaux steppe-savannas. Table 1 gives a preliminary list of plants belonging to each group.

Regarding endemics, their probable origin confirms the contribution of these vegetation types, as well as revealing the possible rôle of plastic mine ecotypes in the speciation of new endemic taxa (Table 2).

The preliminary analysis of the copper-cobalt flora shows that some 81% of the observed species occur in other vegetation types of Upper Shaba. The three main types are steppe-savannas on high plateaux, woodlands of the Xerobrachystegion

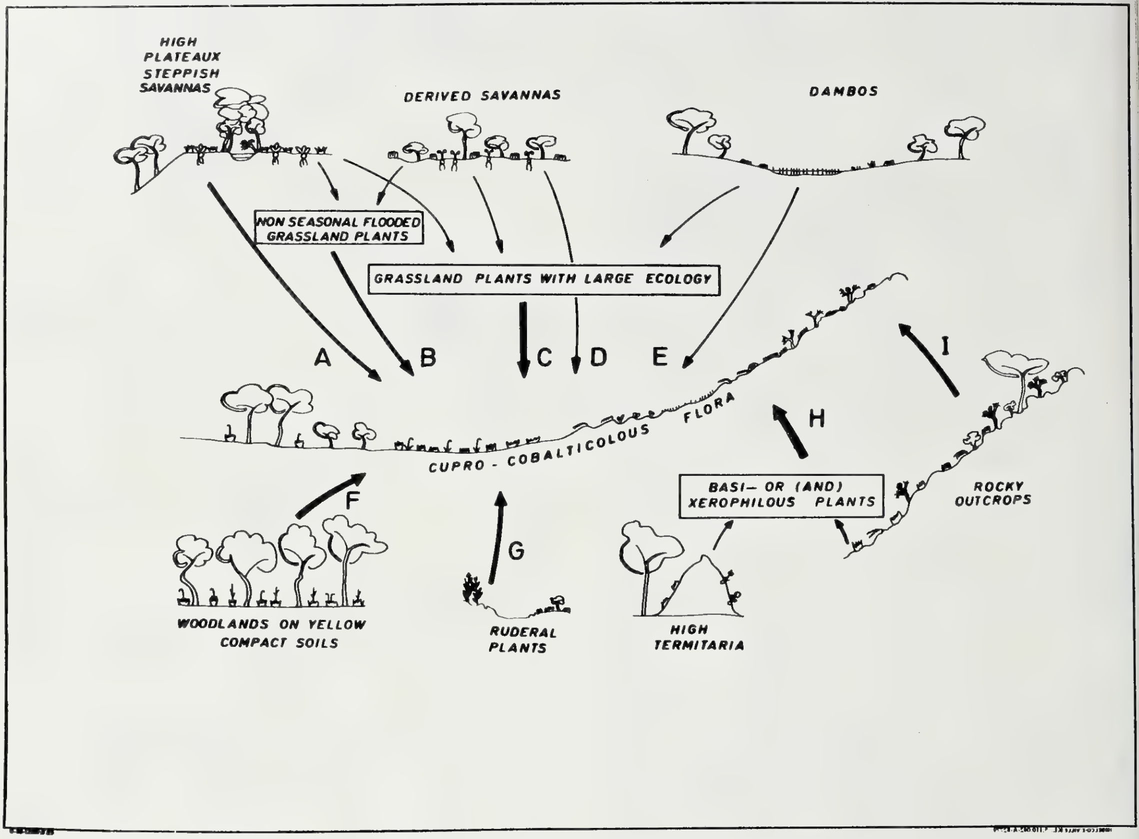
HIGH PLATEAUX STEPPISH SAVANNAS
DERIVED SAVANNAS
DAMBOS
NON SEASONAL FLOODED GRASSLAND PLANTS
GRASSLAND PLANTS WITH LARGE ECOLOGY
A
B
C
D
E
I
H
CUPRO - COBALTICOLOUS FLORA
F
G
BASI– OR (AND) XEROPHILOUS PLANTS
ROCKY OUTCROPS
WOODLANDS ON YELLOW COMPACT SOILS
RUDERAL PLANTS
HIGH TERMITARIA

FIG. 3.— Origin of the copper-cobalt flora of Upper Shaba. Species dealing with the nine groups A to I are listed in the text. N.B. For 'grassland plants with large ecology' read 'grassland plants with wide ecological amplitude'.

Alliance and steppes and bushes on rocky outcrops with three other vegetation types (wooded savannas, dambos, high termitaria) playing a secondary rôle. In total, also taking into account the ruderal plants that are frequent on old mine workings, these nine ecological groups represent about 80% of the flora. The remaining 19% is made up of endemic taxa of varying importance, many of which are derived from characteristic species of neighbouring steppe-savannas, woodlands and rocky outcrops with a second fairly important group derived from mine ecotypes.

EVOLUTION AND SPECIATION IN THE COPPER-COBALT FLORA OF UPPER SHABA

It is generally accepted that most of the copper-cobalt flora is made up of tolerant taxa able to grow on heavy metallic toxic soils. The establishment of metal-resistant plants on copper-cobalt deposits could have favoured the appearance of tolerant taxa, the 'mine ecotypes' of Antonovics *et al.* (1971). These deposits may also have functioned, at some time, as relay stations or secondary centres of origin in the course of migration or distribution of some species. Examples illustrating the hypothesis can be found, for instance, in the genera *Ipomoea* and *Becium*. Plastic species complexes could have evolved and given rise to several ecotypes or slightly different species. Malaisse *et al.* (1983) pinpoint the mechanism of speciation for *Silene cobalticola* originating from the widely distributed *S. burchelli* var. *angustifolia*. Evolution here, results in a reduction of leaf width, an increase in leaf thickness and a reduction or even a disparity in trichome linked to floral differences. Similar evolution has been observed for other species. *Justicia elegantula* S. Moore, for example, another variable species, presents an ecotype with very glabrescent and unusually narrow leaves, which is confined to soils with a high copper content in Zimbabwe (Jacobsen, 1970). In Shaba, speciation of the same plant leads to *Justicia metallorum* (Duvigneaud & Denaeyer-De Smet, 1963). In similar way, *Dicoma anomala* Sond. presents abnormally narrow leaves on rocky copper steppes occurring at Luita, Fungurume and Mashamba. It should be noted that this genus has given rise to an endemic on the serpentine soils of the Great Dyke of Zimbabwe (Wild, 1971). The *Pandiaka carsoni-metallorum* complex gives a further example of evolution and copper ecotype

TABLE 1.— Contribution of different vegetation types to the copper-cobalt flora of Upper Shaba

Major vegetation types

Group A.—High plateaux steppe-savannas

Haumaniastrum polyneurum (S. Moore) Duvign. & Plancke
Triumfetta likasiensis De Wild.
Gladiolus actinomorphanthus Duvign. & Van Bockst.
Gladiolus ledoctei Duvign. & Van Bockst.
Crotalaria diloloensis Bak. f.
Gnidia hockii De Wild.
Thesium pawlowskianum Lawalrée
Crassula vaginata Eckl. & Zeyh.
Crotalaria variegata Welw. ex Bak.
Gnidia kraussiana Meissner var. *molissima* (E.A. Bruce) A. Robyns
Sopubia densiflora Skan
Eriospermum abyssinicum Bak.

Group B.—Non-seasonal flooded grassland plants (including wooded savannas)

Buchnera henriquesii Engl.
Hibiscus rhodanthus Gürke
Uapaca robynsii De Wild.
Crotalaria cornetii Taub. & Dewèvre

Group C.—Grassland plants with wide ecological amplitude

Loudetia simplex C. E. Hubbard
Monocymbium ceresiiforme (Nees) Stapf
Pentanisia schweinfurthii Hiern
Sebaea microphylla (Edgew.) Knobl.
Diheteropogon emarginatus (De Wild.) Robyns
Loudetia superba D. N.
Tristachya thollonii Franch.
Tristachya helenae Buscalioni & Muschler
Ctenium concinuum Pilger
Wahlenbergia capitata (Bak.) Thulin
Gnidia kraussiana Meissner var. *kraussiana*

Group D.—Derived savannas

Monadenium discoideum Bally
Euphorbia zambesiana Benth.
Cryptosepalum maraviense Oliv.

Group E.—Dambos

Thesium quarrei Robyns & Lawalrée
Alectra sessiliflora (Vahl) O. Ktze var. *senegalensis* (Benth.) Hepper

Group F.—Woodlands on yellow compact soils

Triumfetta dekindtiana Engl.
Triumfetta digitata (Oliv.) Sprague & Hutch.
Nephrolepis undulata (Afz. ex Sw.) J. Sm.
Buchnera quadrifaria Bak.
Adenodolichos rhomboideus (O. Hoffm.) Harms
Alloteropsis semialata (R. Br.) Hitchc. var. *ecklonii* (Eyles) Stapf
Olax obtusifolia De Wild.
Tinnea coerulea Gürke
Oxalis obliquifolia Steud. ex A. Rich.
Aeschynomene pygmaca Welw. ex Bak. var. *hebecarpa* J. Léonard
Eriosema englerianum Harms

Group G.—Ruderal plants

Tithonia diversifolia Gray
Arthraxon quartinianus (A. Rich.) Nash
Physalis peruviana L.
Coreopsis oligoflora Klatt
Schizachyrium exile Hochst.
Celosia trigyna L.
Setaria pallide-fusca (Schum.) Stapf & Hubbard
Trema orientalis (L.) Blume
Wahlenbergia collomioides (A. DC.) Thulin

Group H.—Basiphilous or (and) xerophilous plants

Begonia princeae Gilg var. *princeae*
Anemia angolensis Alston
Selaginella abyssinica Spring

Group I.—Rocky outcrops

Euphorbia fanshawei Leach
Batopedina pulvinellata Robbrecht
Mohria lepigera (Bak.) Bak.
Actiniopteris pauciloba Pic. Serm.
Pellaea pectiniformis Bak.
Cheilanthes inaequalis (Kuntze) Mett. var. *inaequalis*
Dichaetanthera shuilinguiana Duvign.
Xerophyta equisetoides Bak. var. *trichophylla* (Bak.) L. B. Smith & Ayensu
Pellaea longipilosa Bonap.
Aeolanthus saxatilis Duvign. & Denaeyer

Minor vegetation types

Forest galleries (banks of rivers)

Pteris vittata L.

High plateaux narrow fringing forest

Delphinium dasycaulon Fresen

speciation (Fig. 4). On copper outcrops, in Shaba, we have observed a range of forms originating from a broad leaf bearing two types of hair, which was observed at Chabara and Dikulushi among other sites, and giving rise to an ecotype with narrow, glabrous leaves occurring at Luiswishi.

Such evolution may or may not be linked to particular, different accumulation level of copper by each taxon. Among the endemics, numerous hyperaccumulator species are found (Brooks *et al.* 1980): nine of the twelve copper hyperaccumulators and five of the fifteen cobalt hyperaccumulators are actually listed i.e. more than a quarter of the endemics. The acquisition of such an adaptation may constitute the first step in new ecotype speciation. Thus the *Buchnera henriquesii* plants occurring at the Etoile Mine possesses a very high copper content, whereas those found at Mindigi or Chabara have low copper values. In a similar way, the *Pandiaka metallorum* plants of Fungurume accumulate ten times more copper than those of Luiswishi, both growing on soils of the same toxic level. Further research, comparing plants grown from seeds of different origin, is the next step in finding solutions to these speciation problems.

TABLE 2.—Origin of copper-cobalt endemics of Upper Shaba

Copper-cobalt endemics		Nearest taxa	
Taxa	Number of ore deposits where observed	Taxa	Vegetation type
Wahlenbergia ericoidella (Duvign. & Denaeyer) Thulin	2	*W. upembensis* Thulin	High plateau steppe-savanna
Haumaniastrum timpermanii (Duvign. & Plancke) Duvign. & Plancke ssp. *kambovianum* (Duvign. & Plancke) Duvign. & Plancke	2	*H. timpermanii* (Duvign. & Plancke) Duvign. & Plancke) subsp. *timpermanii*	High plateau steppe-savanna
Justicia metallorum Duvign.	5	*J. elegantula* S. Moore	High plateau steppe-savanna
Gutenbergia cuprophila Duvign.	2	*G. gossweileri* S. Moore	High plateau steppe-savanna
Sopubia neptunii Duvign. & Van Bockst.	4	*S. conferta* S. Moore	High plateau steppe-savanna
Silene cobalticola Duvign. & Plancke	1	*S. burchelli* Otth. var. *angustifolia* Sond.	High plateau steppe-savanna + derived savanna
Cyperus kibweanus Duvign.	4	*C. margaritaceus* Vahl.	Derived savanna
Faroa chalcophila P. Taylor	2	*F. affinis* De Wild.	Grassland + rocky outcrop
Pandiaka metallorum Duvign. & Van Bockst.	±30	*P. carsoni* (Bak.) Clarke	Dambo
Lapeirousia erythranta (Klotzsch ex Klatt) Bak. var. *welwitschii* (Bak.) Marais ex Geerinck et al.	6	*L. erythranta* (Klotzsch ex Klatt) Bak. var. *briartii* (De Wild. & Th. Dur.) Geerinck et al.	Woodland
Lopholaena deltombei Duvign.	8	*L. alata* Duvign.	Woodland
Sopubia metallorum Duvign.	±15	*S. myomboensis* Duvign. & Van Bockst.	Woodland
Xerophyta demeesmaekeriana Duvign. & Dewit	3	*X. equisetoides* Bak. var. *trichophylla* Bak.	Rocky outcrop
Streptocarpus rhodesianus S. Moore var. *perlanatus* Duvign.	1	*S. rhodesianus* S. Moore var. *rhodesianus*	Rocky outcrop
Icomum biformifolium De Wild.	2	*I. lineare* Burkill	Rocky outcrop.
Icomum tuberculatum De Wild.	7	*I. lineare* Burkill	Rocky outcrop
Crotalaria françoisiana Duvign. & Timp.	1	*C. peschiana* Duvign. & Timp.	Copper outcrop.
Haumaniastrum robertii (Robyns) Duvign. & Plancke	±20	*H. katangense* (S. Moore) Duvign. & Plancke	Copper outcrop
Acalypha dikuluwensis Duvign. & Dewit	1	*Acalypha cupricola* Robyns	Copper outcrop
Buchnera rubriflora Duvign. & Van Bockst.	4	*B. duvigneaudii* Malaisse	Copper outcrop
Becium peschianum Duvign. & Plancke	5	*B. aureoviride* Duvign.	Copper outcrop
Becium empetroides Duvign.	±5	*B. ericoides* Duvign. & Plancke	Copper outcrop
Lindernia perennis Duvign.	1	*Lindernia damblonii* Duvign.	Copper outcrop

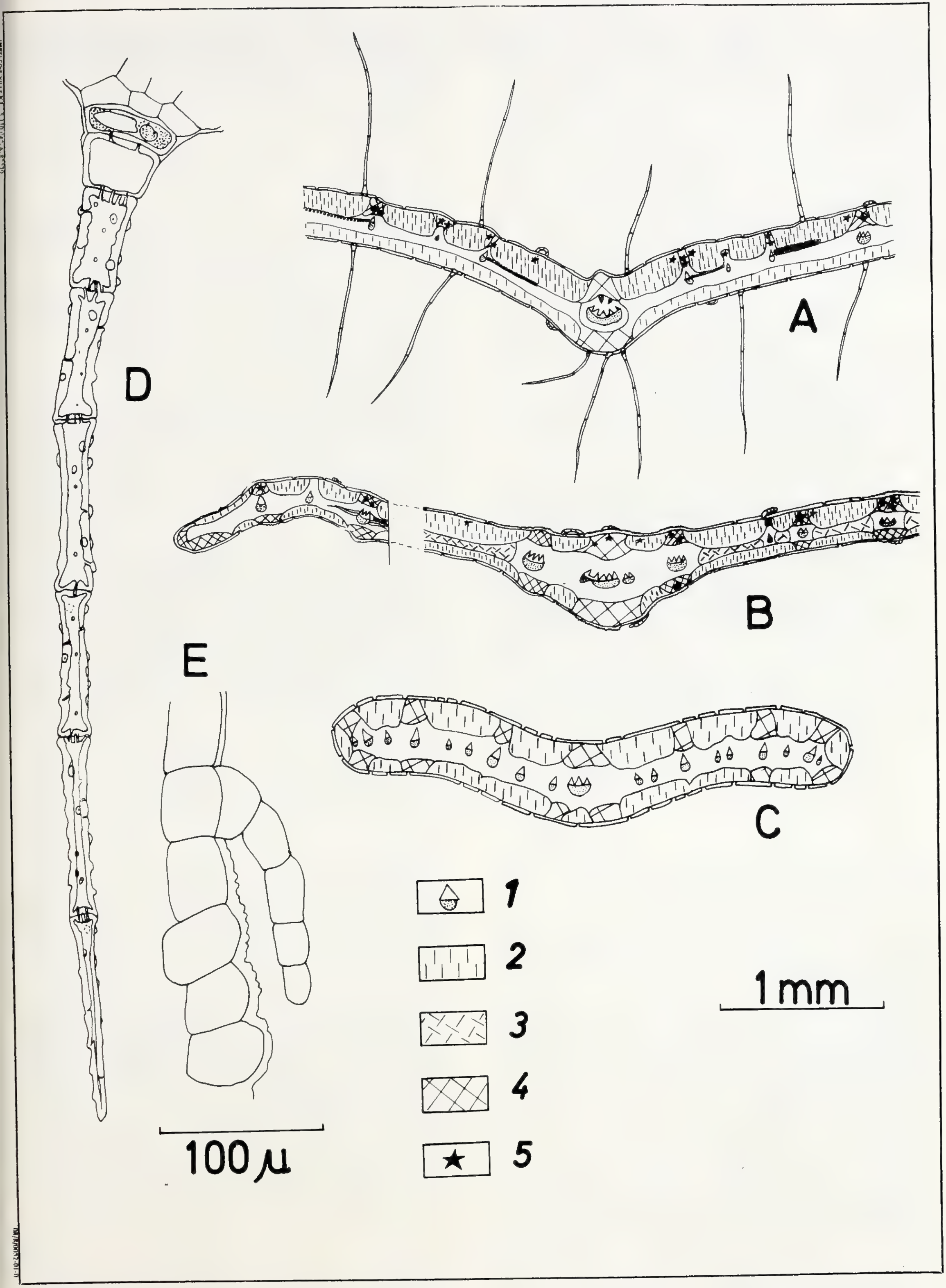

FIG. 4.— Evolution and speciation in the *Pandiaka carsoni-metallorum* complex. Transversal section of leaf and detail of hair for *Pandiaka* from various origins: Chabara (A,D); Kahungwe (B,E); Luiswishi (C). Conventional signs are: 1, vascular bundle; 2, green-leaved palisade parenchyma; 3, green-leaved lacunose parenchyma; 4, collenchyma; 5, calcium oxalate grains and crystals.

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Tendencies in the geographical distribution of the genus *Mariscus* (Cyperaceae) in southern Africa*

P. J. VORSTER**

ABSTRACT

The genus *Mariscus* occurs over practically the whole of the Flora of Southern Africa (FSA) region, with the exception of the west coast and the Karoo region of the Cape Province. Practically no species occur under conditions of less than 250 mm of rain per annum, whereas the highest concentrations of subgenera/sections and species occur where the annual rainfall is more than 500 mm. All the species in the region are summer rainfall plants, or if they occur in the winter rainfall area they behave like summer rainfall plants. The different subgenera/sections recognized within the genus differ widely in respect of their water requirements, yet there is a general concentration of taxa in the eastern part of the country where the rainfall is higher than in the west. Nevertheless, the highest concentrations of taxa are not in the areas of highest rainfall, which suggests that topographical diversity is probably the most important factor determining concentrations of taxa.

The geographical distribution of each subgenus/section in the FSA region is explained in relation to the total distribution of the subgenus/section. The possible climatic or environmental conditions which may determine the distribution of each subgenus/section are mentioned, and the concentration of species within each subgenus/section is demonstrated by means of maps.

RÉSUMÉ

TENDANCES DANS LA DISTRIBUTION GÉOGRAPHIQUE DU GENRE MARISCUS *(CYPERACEAE) EN AFRIQUE AUSTRALE*

Le genre Mariscus *se rencontre pratiquement dans l'entièreté de la flore d'Afrique australe, à l'exception de la région côtière de l'Ouest et de la région du Karoo dans la province du Cap. Pratiquement aucune espèce ne se trouve sous des conditions de moins de 250 mm de pluie par an, tandis que les concentrations les plus élevées de sous-genres/sections et espèces se recontrent la où les précipitations annuelles sont de plus de 500 mm. Toutes les espèces dans la région sont des plantes de régime pluvial estival, ou, si elles surviennent dans la région à pluies d'hiver, elles se comportent comme des plantes de régime pluvial estival. Les différentes sous genres/sections reconnus dans le genre diffèrent largement en ce qui concerne leur nécessité en eau, et pourtant il y a une concentration générale des taxa dans la partie orientale du pays où les chutes de pluies sont plus élevées qu'à l'Ouest. Néanmoins, les concentrations de taxa les plus élevées ne sont pas dans les régions où la densité de pluies est la plus élevée; ce qui suggère que la diversité topographique est probablement le facteur le plus important qui détermine la concentration des taxa.*

La distribution géographique de chaque section/sous genre dans la région floristique de l'Afrique du Sud est expliquée en relation avec la distribution totale de la section/sous genre. Les conditions climatiques et de milieu éventuelles qui peuvent déterminer la distribution de chaque section/sous genre sont mentionnées et les concentrations des espèces dans chaque section/sous genre sont démontrées à l'aide de cartes.

The aim of the present paper is to describe the geographical distribution of the genus *Mariscus* in the Flora of Southern Africa region, and to correlate this distribution pattern with environmental conditions and the taxonomic interrelationships within the genus.

The genus *Mariscus* has, at various times in the past, been recognized as a separate genus, or as a section or subgenus of the genus *Cyperus*. It is characterized by bisexual florets, three stamens, three style branches, no hypogynous scales or bristles, and spikelets which are shed in their entirety. The latter characteristic distinguishes it from *Cyperus*, where the florets and glumes are shed but the rachillae of the spikelets remain attached to the plant. Taking into account the large size and heterogeneity of *Cyperus*, the present tendency to subdivide genera in the family Cyperaceae, and the general distinctiveness of *Mariscus*, the latter is here recognized as a separate genus.

The species which are at present placed in the genus *Mariscus* occur over practically the whole of the Flora of Southern Africa region (Fig. 1), but are absent from the west coast and the semi-desert Karoo area of the Cape Province. This wide distribution is a manifestation of the adaptation of groups within the genus to widely differing habitat types. Once this adaptation had been accomplished to some degree, it resulted in spatial separation of the taxa, and this geographical separation together with the evolutionary pressure excerted by the different habitat types, must rapidly have resulted in the different groups of species which can be recognized today. Definite evolutionary lines can be distinguished, which are correlated with habitat preference.

The supraspecific groups within the genus *Mariscus* were given the rank of subgenus or section, and each is characterized by the morphology of the basal parts and inflorescence. The morphology of the basal parts are considered to be of great

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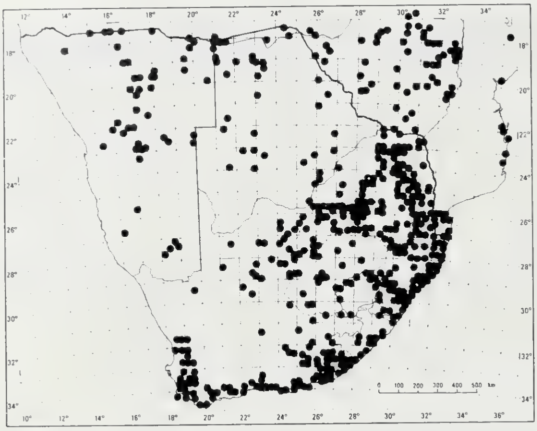

FIG. 1.—Genus *Mariscus:* map showing known geographical distribution in FSA area.

taxonomic importance, because this is the factor which enables the plants to live under specific conditions of soil moisture. The anatomical distinctiveness of the subgenera and sections indicates that these taxa are natural, and not merely the result of morphological convergence caused by similar environmental pressures on the different species within each of the presently recognised groups.

In the course of my revisionary work on the South African species of *Mariscus,* the species were grouped into the subgenera and sections listed below. As the recognition of some of these subgenera and sections in the genus *Mariscus* requires nomenclatural changes, this matter is treated elsewhere. For the purpose of the present paper those names which have not yet been validated, are printed between quotation marks. The following supraspecific taxa are recognized:

1. Subgenus '*Decidui*'
2. Subgenus '*Thunbergiani*'
3. Subgenus '*Umbellati*'
   a. Section *Umbellati*
   b. Section '*Latespica*'
   c. Section '*Laxigluma*'
4. Subgenus *Bulbocaulis*
5. Subgenus '*Tunicati*'

From the distribution records given for species by Kükenthal (1936), *Mariscus* is clearly a genus of tropical and subtropical regions, with the number of species rapidly diminishing further than 30° from the equator. This global situation also holds good for southern Africa, where the largest concentrations of species and individuals are found in the warm, moist eastern third of the country (Fig. 3). Its absence from the west coast and the Karoo region can be correlated to an annual rainfall of less than 250 mm. It is also absent from a large area where the borders of the Cape Province, South West Africa/Namibia and Botswana meet. The latter area constitutes deep sandy soil and semi-desert conditions, and it is uncertain whether the lack of records should be attributed to poor collecting or to low rainfall.

As far as subgenera and sections are concerned, the higher concentrations of these taxa occur in the eastern part of the country (Fig. 2). The highest concentrations of subgenera and sections have not been recorded right at the coast in the areas getting the highest rainfall, but rather some distance inland. These concentrations are found along the escarpment, where a wide variety of habitats are available over a short distance. Therefore the highest concentration of subgenera and sections has been recorded in the area around Pretoria, which does not have a particularly lush vegetation and receives a mere 700 mm of rain per annum compared with up to twice as much along parts of the east coast and the eastern escarpment. Yet the Pretoria area offers over a short distance places receiving severe winter frost as well as virtually frost-free niches, marshy streamside situations to deep, dry sand or shallow humus-rich soil over flat rock slabs under intense insolation, and exposed sites to dense ravine forest. Moreover, this area is centrally situated in relation to the distribution areas of the individual subgenera and sections, so that the colonization of the different habitats would not require any great problem of migration.

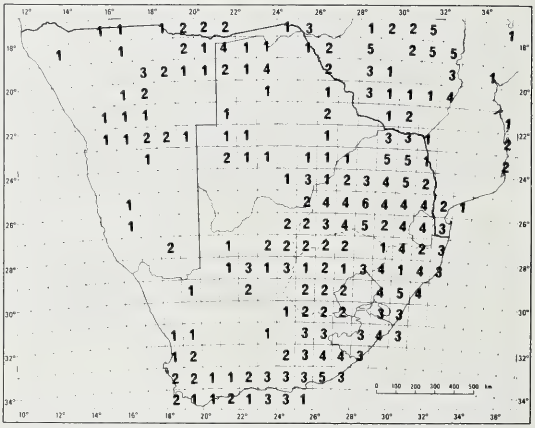

FIG. 2.—Genus *Mariscus:* map showing known concentration of subgenera/sections in FSA area.

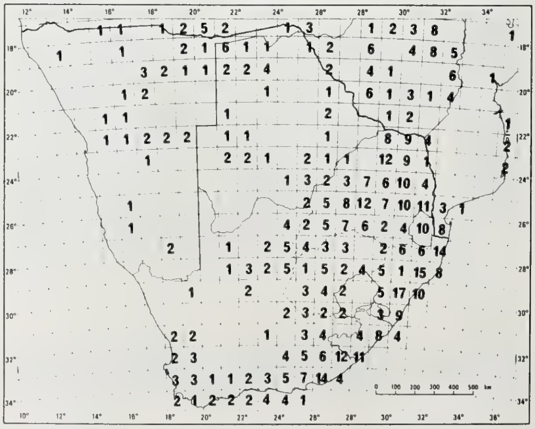

FIG. 3.—Genus *Mariscus:* map showing known concentration of species in FSA area.

In general terms, winter temperatures are probably not particularly restrictive in the geographical distribution of the genus, as all the southern African species (except two inhabitants of evergreen forest) die back to their basal parts during winter. Nevertheless it is conspicuous that certain species are restricted to areas receiving little or no frost during winter, and no species have been recorded from areas which receive snow during winter, such as the high Drakensberg escarpment between Lesotho and Natal. Most species seem to thrive under high summer temperatures as befits an essentially tropical genus, but a number of species show a definite preference for temperate or cool summer conditions. Not surprisingly, these species are mostly endemic in the region under discussion. The concentration of subgenera/sections as well as species in the moister eastern part of the country and their absence where the annual rainfall is less than 250 mm, leaves the impression that *Mariscus* is a hygrophyllous genus in general. It is, however, noteworthy that there is wide individual variety in this respect, with some species growing only in wet soil, whereas others are pronounced xerophytes and grow only in the driest, best-drained places, even within areas of high rainfall.

The genus is a typical summer-rainfall one, and the presence of three species in the south-western Cape fynbos which receives its rain mostly during winter, must be ascribed to migration from the summer rainfall area. It is noteworthy that all three species which occur under winter rainfall conditions also occur in the adjacent summer rainfall area, and that they behave like summer rainfall plants in the sense that they grow actively during summer but die back during winter. These species are, however, independent of rainfall for their water supply, as they occupy riverside habitats which are wet throughout the year.

The subgenus *'Decidui'* (*Cyperus* sect. *Decidui* Kükenth.) has a horizontal sub-underground rhizome, 2–3 mm in diameter, consisting of spherical nodes connected to each other by thinner runners. This is a common base type amongst hydrophyllous Cyperaceae, and the sole species, *Mariscus deciduus* (Boeck.) C.B. Cl., is indeed confined to stream banks and similar wet habitats where it occurs between other grassy vegetation. As a low heliophyte (about 500 mm high) it is restricted to short grassland on cool highlands. It is known from *ca.* 10½°S in Zaïre to 29°S in Natal, wherever there is short grassland on streambanks. This area is probably temperate in summer, and winter frost is light or absent. (Fig. 4).

The subgenus *'Thunbergiani'* (*Mariscus* sect. *Thunbergiani* C.B. Cl.) has rather massive and hard rhizomes with nodes crowded together and covered with old leaf bases. The plants are medium-sized to large (up to 2 m high), and are usually found in streamside habitats on rather wet soil. In all the species the glumes contain a brown to reddish-brown pigment. Kükenthal (l.c. 430) amplified Clarke's original circumscription of the erstwhile section by including species from North, Central and South America, the West Indies, Ascension Island, Madagascar and Australasia. I have not seen any authentically named material of these species, and as Kükenthal erroneously (in my opinion) included *M. congestus* (Vahl) C.B. Cl. in this section, it may indicate that the non-southern African addition to the section is anomalous. I have neither seen any material which could be placed in this subgenus from any of the areas mentioned above. In southern Africa this subgenus is represented by 7 species, which are all endemic. Four of these have rather restricted distribution areas, whereas the other three occupy larger areas, one of which includes nearly the total distribution area of the subgenus in southern Africa. The plants all occur in temperate to subtropical streambank situations in areas which are frost free or getting only very light frost. As a result of their streamside habitats, the distribution of these species is probably independent from rainfall, and it is not impossible that low winter temperatures is the restrictive factor in their distribution. In southern Africa the suitable habitats coincide with a narrow zone along the entire eastern and southern coast and extending northwards along the escarpment parallel to the coast to as far north as 17½°S. It occurs further inland along the eastern and northern Transvaal escarpment and the highlands of eastern and northern Zimbabwe. One species, *M. thunbergii* (Vahl) Schrad., is very common in the winter rainfall area of the south-western Cape Province, extending eastwards along the south coast into the summer rainfall region where its place is taken by another species. Still another species, *M. tabularis* (Schrad.) C.B. Cl., occurs in one enclave in the winter rainfall area of the south-western Cape and in another enclave in the eastern Cape, separated by a gap of some 400 km; yet the plants of the two areas are virtually identical. Two types of basal morphology are found in this subgenus. In the first group of four species the rhizome is horizontal, and the plants tend to form extensive clones of more or less spaced

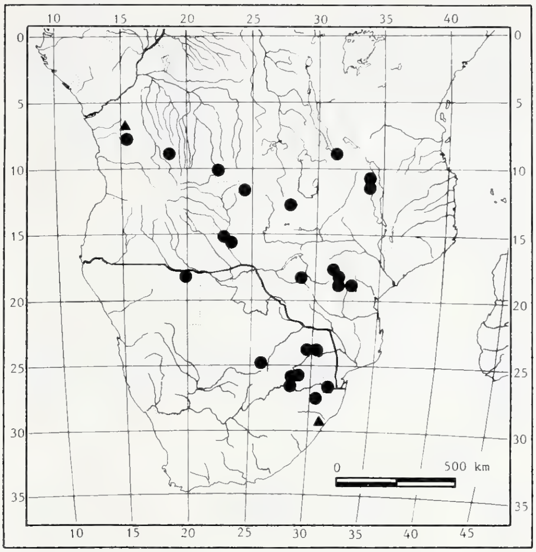

FIG. 4.—*Mariscus* subgen. *'Decidui'*: map showing total known geographical distribution of the sole species, *M. deciduus* (Boeck.) C.B. Cl.

individual aerial plants which are linked together by their rhizomes. These species all occur in grassland, in direct sunlight. In the second group of three species the rhizomes are vertical and the plants form dense tufts. Two of these species occur in glades in evergreen montane or coastal forest, while the third, known from only a single gathering, was found in short montane grassland under cool climatic conditions. If the southern African species are considered to constitute an endemic subgenus, which is strongly suspected of being the case, an analysis of species concentration reveals that the largest concentration of species occurs in the vicinity of Grahamstown, where 5 of the 7 species have been recorded. It would not be unreasonable to consider this area to be the subgeneric centre of distribution. (Fig. 5).

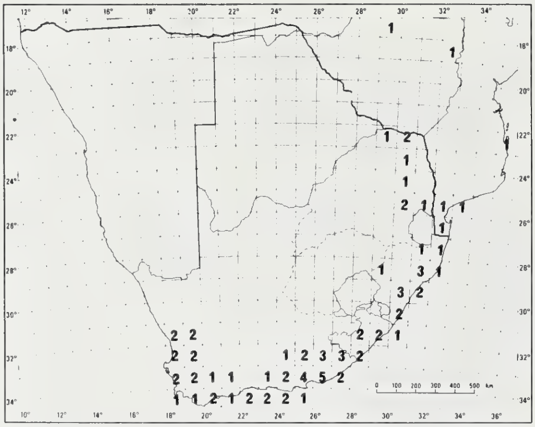

FIG. 5.—*Mariscus* subgen. *'Thunbergiani'*: map showing known geograpical distribution, and concentration of species, in FSA area.

The subgenus *'Umbellati'* has spherical or tear-shaped basal parts, 5–10 mm in diameter and clad in leaf bases. Vegetative propagation is by means of lateral innovations which are formed outside the enveloping sheath of leaf bases around the older base. The plants are medium-sized and the inflorescence is a simple or compound umbel. This concept consists of three clearly separate entities, yet they are united by their common base type and the general architecture of the inflorescence to such an extent that I have placed them in the same subgenus, albeit in three separate sections. On account of their identical basal parts one would expect the three sections to have similar water requirements, but in fact they differ considerably.

The first section, *Umbellati* C.B. Cl., consists of small to medium-sized plants, normally 200–500 mm high. The inflorescence is a simple umbel which is extended or may be contracted to varying degrees. The spikelets are terete and one- to few-flowered, and the glumes are green to yellowish-green. Kükenthal *(l.c.* 506 *et seq.)* listed 27 species in this section from the more tropical parts of Africa, the Mascarenes, Asia, Australia, North, Central and South America and the West Indies. This section is decidedly tropical in its requirements, and in southern Africa the species all occur in more or less frost free areas with an annual rainfall of at least 800 mm. This corresponds with the lowlands of Natal and the eastern Cape Province, as well as the Transvaal lowveld and foot of the escarpment (Fig. 6). One species, *M. macer* Kunth, extends into central Transvaal, but is confined to frost-free niches in the hills, where it occurs more or less sheltered in dry ravine forest. These species are all dry land plants, being dependent on rain for their moisture supply, so that their distribution is stricly governed by rainfall patterns. Of the six species recorded in the FSA region, *M. sumatrensis* (Retz.) J. Raynal has the widest distribution, namely throughout the moister parts of tropical Africa and tropical Asia. *M. sublimis* C.B. Cl. and *M. cylindristachyus* Steud. are widespread tropical African endemics, whereas *M. macer, M. macrocarpus* Kunth and an undescribed species have restricted distribution areas. The impression was gained that *M. sumatrensis* may be an introduced weed, and the same may hold true for *M. sublimis* and *M. cylindristachyus* which are known from only a few collections in the FSA region.

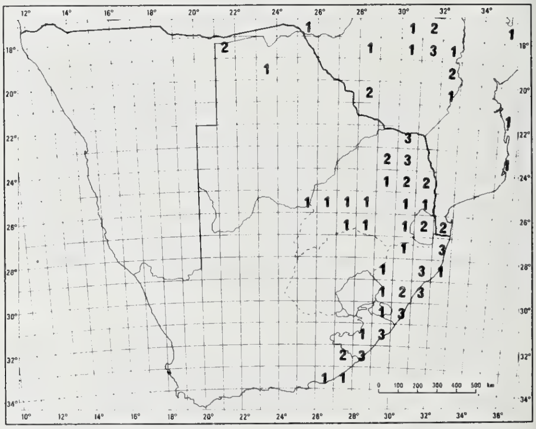

FIG. 6.—*Mariscus* sect. *Umbellati:* map showing known geographical distribution, and concentration of species, in FSA area.

The second section, *'Latespica,'* consists of two medium-sized hydrophytic species, one endemic and one probably an introduced weed. The inflorescence is a compound umbel, the spikelets are laterally compressed and many-flowered, and the glumes are tightly imbricate and have a purple-black pigmentation. Both are generally confined to cool areas or cool niches, where they occur on stream banks or in bogs. The endemic species, *M. congestus,* (Vahl) C.B. Cl., is very common wherever there are suitable habitats in the eastern third of South Africa. Its occurrence in the south-western Cape, South West Africa and Zimbabwe may be the result of its having been introduced into these areas. Its endemism is indeed somewhat surprising, considering the ease with which it established itself in recent times in Europe and Australia. The second species, *M. keniensis* (Kükenth.) S. Hooper, is known from the east African escarpment, from the

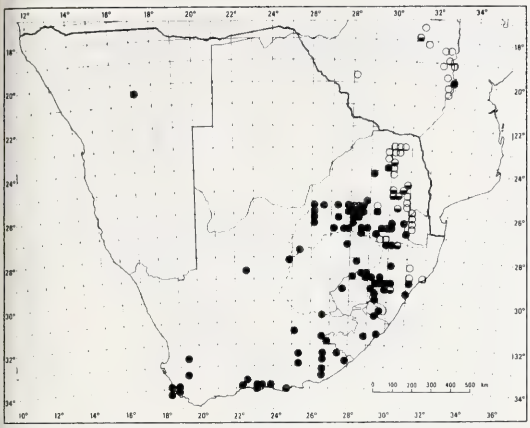

FIG. 7.—Mariscus sect. *'Latespica'*: map showing known geographical distribution in FSA area. ● : *M. congestus;* ○ : *M. keniensis.*

equator southwards to Natal. In southern Africa I have only seen it in association with commercial timber plantations, and it has almost certainly been introduced into this region. Its distribution suggests a requirement for somewhat more tropical conditions than *M. congestus* (Fig. 7).

The third, section, *'Laxigluma'* (*Mariscus* subsect. *Laxiglumae* C.B. Cl.), is represented by a single medium-sized xerophytic species, *M. laxiflorus* Turrill, in the FSA region. Its inflorescence is a compound umbel, the spikelets are laterally compressed and many-flowered, and the straw-coloured glumes are set at an obtuse angle relative to the rachilla. Kükenthal (*l.c.* 458) recognized 23 species in this section, mostly from the dry areas of Central and South America, but also from North America (five species), Sikkim (one species) and Africa (three species). It is tempting to speculate on the representation of this essentially *American* section in Africa. That the species on the two continents are closely related, leaves no doubt, as Kükenthal's illustration of *Cyperus spectabilis* Link from Central America (*l.c.* 460) shows a plant remarkably similar to *M. laxiflorus. M. laxiflorus* occurs from about 4°S in Zaïre to about 26°S in the Transvaal (Fig. 8), usually in dry, tall, open woodland in partial shade, and usually on deep, loose sand. This area becomes hot in summer and is more or less frost free. It receives 500 to 750 mm of rain per annum, concentrated within two or three very hot summer months.

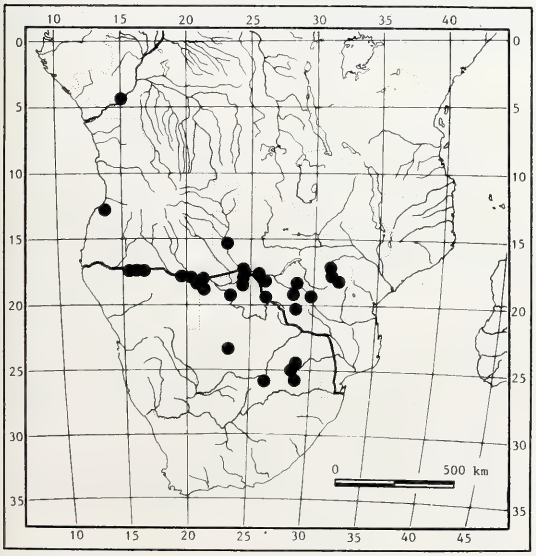

FIG. 8.—*Mariscus* sect. *'Laxigluma':* map showing total known geographical distribution of the species represented in the FSA area, *M. laxiflorus* Turrill.

The subgenus *Bulbocaulis* C.B. Cl. is characterized by narrowly ovate basal pseudobulbs, which comprise somewhat thickened stem bases covered by numerous layers of non-fleshy leaf bases. Unlike the subgenus *'Umbellati,'* vegetative propagation is by means of lateral innovations which are formed within the enveloping sheath of old leaf bases. The plants are small to medium-sized, with a variety of inflorescence types ranging from a compound umbel to a single head-like spike. The glumes have a variety of colours. This is essentially an African subgenus, and practically all 38 species recognized by Kükenthal (*l.c.* 538 *et seq.*) occur in the dry tropical savanna of Africa and Madagascar. Only *M. dubius* (Rottb.) Kükenth. ex G.E.C. Fischer and possibly *M. dregeanus* Kunth extend as far as Asia, the former occurring as far east as the Tonkin province of China, whereas one species (*M. maritimus* Miq.) is endemic to the Philippines. Both *M. dubius* and *M. dregeanus* are confined to tropical regions with an annual rainfall in excess of 700 mm. *M. dubius* especially is often found associated with *M. sumatrensis* of the section *Umbellati,* and it is noteworthy that these two species have a similar distribution pattern in Africa and Asia. The remaining species are all xerophytes to varying degrees, occurring more or less in the open on bare ground or wedged into cracks in rocks, often under extreme insolation in very well-drained niches. Fifteen species are recognized in the FSA area. They occur throughout the summer rainfall region wherever the annual rainfall exceeds 250 mm but, in spite of their xerophytic nature, the highest concentrations of species are along the east coast and eastern excarpment (Fig. 9).

The subgenus *'Tunicati'* (*Cyperus* subsect. *Tunicatae* C.B. Cl. (p.p.?)) is represented in the FSA region by two xerophytic species. Kükenthal (*l.c.* 121) included 8 species in this section, all from Africa but with one species extending through Asia to Australia. The plants are characterized by having a series of underground true bulbs which are interconnected by filiform scale-clad rhizomes. The aerial plants are strictly annual and regeneration in spring takes place from the underground bulbs. The two southern African species have a wide distribution in southern and eastern Africa, where they occur under dry conditions of 260 to 600 mm of rain per annum (Fig. 10). These plants favour more or less open, sunny sites where they occur on loose sandy soil to very hard, stony soil. *'M. fulgens'* (*Cyperus fulgens* C.B. Cl). shows a tendency to

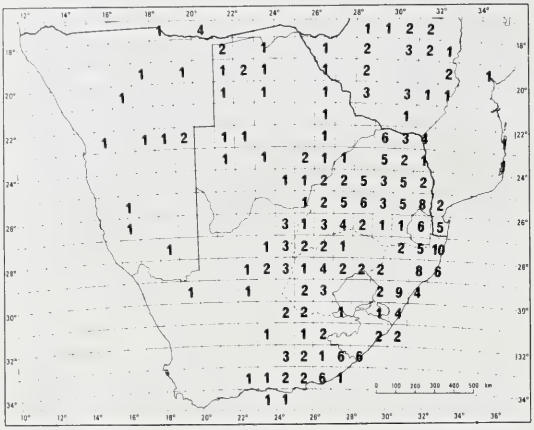

FIG. 9.—*Mariscus* subgen. *Bulbocaulis:* map showing known geographical distribution, and concentration of species, in FSA area.

become a weed in cultivated lands. The wide distribution of both species suggests a considerable degree of adaptibility in respect of environmental requirements. The underground bulbs are almost certainly a mechanism for surviving drought, and the distribution of the southern African species in relation to rainfall patterns suggests that a rainfall of more than about 600 mm per year is a limiting factor in their distribution. This is borne out by observations on cultivated plants. As both species die back completely during winter, it is difficult to envisage winter frost as a limiting factor in their distribution, yet *'M. usitatus'* (*Cyperus usitatus* Burch.) occurs almost five degrees longitude further south than *'M. fulgens.'* and this can only be explained in terms of increased cold resistance.

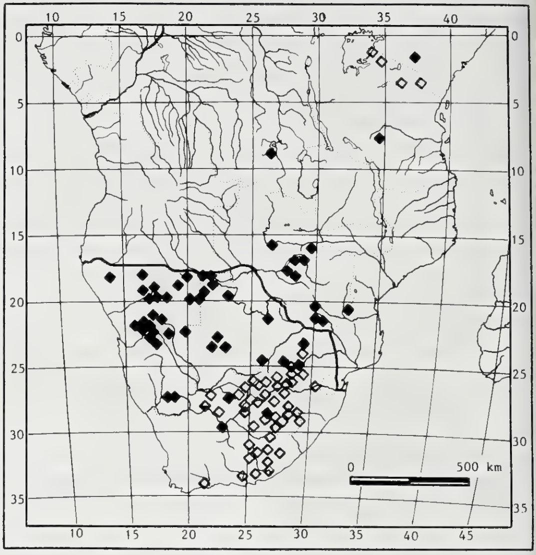

FIG. 10.—*Mariscus* subgen. *'Tunicati':* map showing total known geographical distribution of the two species represented in the FSA area. ◆ : *M. 'fulgens'*; ◇ : *M. 'usitatus'*.

It will be realized that, whereas it is possible to indicate trends in the distribution, pinpoint concentrations, and suggest reasons for the observed distribution patterns of subgenera/sections and species, it would be unwise to speculate on areas of origin of the taxa or past migrations. Clearly the southern African subgenera and sections, if not species, exhibit a low degree of endemism and must be seen as a mere extension of the large pantropical distribution of the genus. It will only be possible to see the southern African taxa in true perspective once the whole genus has been studied, which is unfortunately outside our mandate.

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La flore des massifs Sahariens: espèces illusoires et endémiques vraies

J. -P. LEBRUN*

RÉSUMÉ

Les massifs montagneux qui se dressent au Sahara, à savoir Hoggar, Tassili n'Ajjer, Aïr, Tibesti, Ennedi, Jebel Marra, Gebel Elba, ont exercé sur certains botanistes une véritable fascination. De sorte que l'on a assisté à des naissances successives, et même multiples, d'espèces nouvelles.

Au vrai, la chose peut s'expliquer en partie par le fait que ceux s'intéressant à ces zones, s'ils étaient indubitablement des experts du monde méditerranéen, connaissaient fort peu la flore tropicale africaine.

Il en résulte qu'une certaine littérature botanique, même fort récente (Quézel, 1978; Ozenda, 1977), se trouve encombrée de binoms, simples synonymes de noms plus anciens et par conséquent prioritaires, d'espèces bien connues. D'autant plus que certains auteurs ne se donnent visiblement pas la peine de se tenir au courant de l'évolution des connaissances botaniques grâce à la consultation des travaux les plus récents.

Pourtant, des 85 espèces endémiques reconnues comme telles dans un premier temps : 37 correspondent à de fausses identifications (Tableau 1); 7 ont subi un changement de nom, soit pour des raisons systématiques, soit pour raisons nomenclaturales (Tableau 2); 1 connue seulement du type *(Quezelia)* nécessiterait de nouvelles récoltes; 31 appartenant à des genres difficiles restent à étudier (p. 513); 9 sont de véritables endémiques (p. 514).

Finalement: 'le nombre d'espèces endémiques des enclaves montagnardes des zones sèches nord-tropicales est beaucoup plus faible qu'on ne l'avait cru de prime abord'.

Echantillons et cartes de répartition en main, on peut évaluer actuellement le nombre d'endémiques vraies à 12 espèces.

ABSTRACT

THE FLORA IN THE SOUTHERN SAHARA MOUNTAIN MASSES: ILLUSIVE AND TRUE ENDEMIC SPECIES

The mountain masses in the southern part of the Sahara, namely Hoggar, Tassili n 'Ajjer, Air, Tibesti, Ennedi, Jebel Marra and Gebel Elba, have fascinated botanists to such an extent that there has been successive and even multiple creation of new species.

This situation can be partly explained by the fact that those who were interested in these areas, although undoubtedly world experts in the Mediterranean area, have less knowledge of the African tropical flora.

As a result, certain botanical literature, some quite recent, abounds in binomials, some merely synonyms of older names of well-known species. The problem is aggravated by the fact that a number of authors do not keep up with recent literature.

A breakdown of the 85 species previously accepted as endemics reveals that: 37 were incorrectly identified (Table 1); 7 changed their names either for systematic or nomenclatural reasons (Table 2); 1 is known only from the type (Quezelia) *and requires further collection; 31 belong to difficult genera and require further study (p. 513); and 9 are true endemics (p. 514).*

This study shows that the number of endemic species from the mountainous enclaves in the dry northern-tropical areas is considerably lower than previously estimated. With more material and with the aid of distribution maps, it is now possible to put the number of true endemics at 12 species.

Aurions-nous procédé personnellement aux nombreuses exécutions capitales mentionnées ci-dessus, que nous craindrions de nous voir reprocher d'opposer, de façon par trop simpliste, notre 'lumping' au 'splitting' de certains, et ceci, au mépris du conseil d'Edmond Boissier (nous citons de mémoire) : il vaut mieux séparer que réunir mal à propos.

Mais, les choses ne se présentent pas ainsi. Nous avons simplement tenté de nous tenir au courant, autant que faire se peut, des contributions postérieures aux créations spécifiques envisagées, contributions signées de botanistes de haut niveau, ou de prendre bonne note d'avis éclairés; ceux du cypérologue Raynal, par exemple. Ajoutons que Wickens (1977), en 1977, avait déjà réduit de 56 à 38 le nombre des 'endémiques' du Tibesti décrites par Quézel.

Bien entendu, ceux qui y tiennent, peuvent faire état de ces endémiques et utiliser les binoms correspondants. Mais nous ne les suivrons pas dans cette voie. Nous préférons attendre sagement qu'on en connaisse un peu plus en matière de spéciation; ou que des études nouvelles, très approfondies, apportent des arguments décisifs en faveur de certains des taxons auxquels nous ne reconnaissons pas actuellement le rang de macro-ni même de microendémiques.

Il est peut-être passionnant, sinon récréatif, de distinguer une entité par sommet; *Bromus garamas* au Hoggar, *B. tibesticus* au Tibesti, *B. sinaicus* au Sinai, *B. adoensis* en Ethiopie. La chose a été faite chez les *Dendrosenecio* d'Afrique orientale; actuellement, on tend à réduire le nombre de taxons de rang spécifique dans ce groupe (Mabberley, 1973).

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De plus, il n'est pas acceptable de décrire des espèces nouvelles sur des échantillons insuffisants; c'est pourtant parfois malheureusement le cas, encore actuellement, même dans des genres difficiles. Citons par exemple, d'Afrique tropicale:

Cissus okoutensis Berhaut (plante stérile), *Smithia ? trochainii* Berhaut également stérile; le premier n'est probablement qu'une repousse restée sans fleurs d'un *Vitis* introduit, peut-être très anciennement, au Sénégal; le second est un morceau d'*Aeschynomene crassicaulis* Harms. De la même manière, dans la zone qui nous intéresse ici, *Bergia mairei* et *Nigripteris quezelii* ne sont que des échantillons mal venus d'espèces bien connues. *Alhagi brevispinum* n. sp.? Maire fut basé sur des échantillons stériles.

Quelques plantes qui avaient été décrites au début des investigations dans les massifs sahariens sont tombées depuis longtemps en synonymie et nous ne les avons pas citées ici; c'est le cas, par exemple, de *Dichilus dallonianus* Maire [=*Argyrolobium abyssinicum* Jaub. et Spach; plus correctement: *A. arabicum* (Decne) Jaub. et Spach, vide Polhill, 1968]; d'autres ont été reclassées à des rangs inférieurs; c'est le cas du *Fagonia tilhoana* Maire que son créateur a rattaché au *F. arabica* L. à titre de simple variété.

TABLEAU 1.— Liste des pseudo-espèces des enclaves montagnardes des zones sèches nord-tropicales avec les noms corrects des espèces dont elles sont synonymes

Noms des pseudo-espèces	Noms corrects
Albuca septentrionalis Quézel	Albuca sudanica *A. Chev.* fa. réduite
Avena tibestica Bruneau de Miré et Quézel	Helictotrichon elongatum *(Hochst. ex A. Rich.) Hubb.*
Bergia mairei Quézel	Bergia suffruticosa *(Del.) Fenzl*
Bromus garamas Maire	Bromus pectinatus *Thunb.*
Bromus tibesticus Maire	Bromus pectinatus *Thunb.*
Caralluma venenosa Maire	Caralluma decaisneana *(Lem.) N.E. Br.*
Centaurium minutissimum Maire	Centaurium pulchellum *(Swartz) Druce*
Clematis tibestica Quézel	Clematis hirsuta *Guill. et Perr.*
Coelachyrum oligobrachiatum A. Camus.	Coelachyrum brevifolium *Nees*
Commicarpus montanus Bruneau de Miré, Gillet et Quézel	probablement Commicarpus grandiflorus *(A. Rich.) Standl.*
Chloris tibestica Quézel	Chloris virgata *Swartz*
Crassula tibestica Bruneau de Miré et Quézel	Crassula schimperi *C.A. Mey.*
Dichrocephala tibestica Quézel	Dichrocephala chrysanthemifolia *(Blume) DC.*
Epilobium mirei Quézel	Epilobium hirsutum *L.*
Festuca tibestica Bruneau de Miré et Quézel	Festuca abyssinica *Hochst. ex A. Rich.*
Fimbristylis marrana Bruneau de Miré et Quézel	Bulbostylis densa *(Wall.) Hand.-Mazz.*
Fimbrystylis minutissima Maire	Bulbosylis densa *(Wall.) Hand.-Mazz.*
Glossonema gautieri Batt. et Trabut	Glossonema boveanum subsp. nubicum *(Decne.) Bull.*
Heleocharis tibestica Quézel	Eleocharis caduca *(Del.) Schultes*
Lotus tibesticus Maire var. *fallax* Maire	Lotus jolyi *Batt.*
Lupinus tassilicus Maire	Lupinus digitatus *Forskal*
Nigripteris quezelii Tard.-Blot.	Cheilanthes maderensis *Lowe*
Oropetium tibesticum Gillet et Quézel	Oropetium capense *Stapf*
Oropetium ennedicum Gillet et Quézel	Oropetium minimum *(Hochst.) Pilger*
Pegolettia dubiefiana Quézel	Pegolettia senegalensis *Cass.*
Phagnalon tibesticum Chevassut et Quézel subsp. *tibesticum*	Phagnalon scalarum *Schweinf. ex Schwartz*
Pluchea crenata Quézel	Conyza pyrrhopappa *Schultz Bip. ex A. Rich.*
Pulicaria lhotei Maire	Pulicaria arabica *(L.) Cass.*
Rhynchosia airica Bruneau de Miré et Gillet	Rhynchosia totta var. venulosa *(Hiern) Verdc.*
Rhynchosia tibestica Bruneau de Miré, Gillet et Quézel	Rhynchosia totta var. venulosa *(Hiern) Verdc.*
Sonchus tibesticus Quézel	Sonchus asper *(L.) Hill*
Spergula fontenellei Maire	Spergularia microsperma *(Kindb.) Fouc. ex Monn. emend.**
Spergula tibestica Quézel et Monnier	Spergularia microsperma *(Kindb.) Fouc. ex Monn. emend.**
Tibestina lanuginosa Maire	Dicoma capensis *Less.*
Trichodesma giganteum Quézel	Trichodesma africanum *(L.) Lehm.*
Trichodesma gracile Batt. et Trab.	Trichodesma africanum *(L.) Lehm.*
Lotus borkouanus Quézel	Lotus arabicus *L.*

*Validité douteuse, il existe un Spergularia microsperma *(Kindb.) Vved.*

TABLEAU 2.—Liste des espèces des massifs sahariens ayant fait l'objet de changements nomenclaturaux

Nom ancien	Nom correct actuel
Fagonia flamandi Batt.	Fagonia tenuifolia *Hochst. et Steud. ex Boiss.* (endémique)
Monodiella flexuosa Maire	Centaurium flexuosum *(Maire) Lebrun et Marais* (endémique)
Silene hoggariensis Quézel	Silene lynesii *Norman*
Silene kiliani Maire	Silene lynesii *Norman*
Tripogon tibesticum de Miré, Gillet et Quézel	Tripogon multiflorus *de Miré et Gillet* (endémique)
Wahlenbergia bernardi Leredde	Wahlenbergia campanuloides *(Del.) Vatke*
Wahlenbergia tibestica Quézel	Wahlenbergia campanuloides *(Del.) Vatke*

Certes, et nous le savons bien, la notion d'espèce est difficile à définir et à appréhender. Elle varie selon les auteurs, elle est subjective. Et personnellement, nous n'y échappons pas. Cependant, dans le cas des montagnes sahariennes, il eut été préférable, en face de variations mineures constatées sur des échantillons de cette provenance, de décrire des sous-espèces plutôt que des espèces. Ce qui n'a pas été fait.

QUELQUES CONSÉQUENCES DE L'ÉTUDE CRITIQUE DES PSEUDO-ESPÈCES DES MONTAGNES SAHARIENNES

1. *Il n'est plus possible de conserver* et de tenir compte d'affirmations et de déductions, reposant purement et simplement sur de fausses identifications et des rapprochements hasardeux.

Citons-en simplement une parmi d'autres: 'La mise en place de cette flore (celle du Toussidé au Tibesti) pose de singuliers problèmes'. (Bruneau de Miré & Quézel, 1959). Il s'agit d'un massif édifié il y a une dizaine de millénaires. Par conséquent, il y aurait eu individualisation d'endémiques dans un laps de temps assez court. Les choses deviennent beaucoup plus simples et probablement plus proches de la réalité si l'on estime qu'il n'y a pas d'endémiques.

Simplement, à cause d'un milieu très particulier (fumerolles, lappiaz), des espèces s'y présentent sous des formes réduites ou curieuses, s'éloignant sensiblement des échantillons récoltés ailleurs. C'est bien ce que souligne Guittonneau (1972) à propos de l'*Erodium oreophilum.*

Le statut véritable de certaines endémiques ou supposées telles reste encore à établir. Cela se fera au fur et à mesure des révisions d'ensemble. Mais des difficultés surgiront dans plusieurs cas, simplement parce que le matériel botanique actuellement accessible est parfois extrêmement réduit. Wickens le souligne dans le cas du *Phagnalon tibesticum* subsp. *meridionale.* De nouvelles récoltes s'imposent, mais actuellement, la situation ne s'y prête pas, du moins dans certaines zones, au Tibesti en particulier. On ne peut que le déplorer en attendant patiemment des jours meilleurs.

2. *Liste des taxons*

A notre connaissance, la liste des taxons de rang spécifique encore critiques, s'établit comme suit:

Agrostis tibestica Quézel
Amphinomia (Lotononis) riouxii Quézel*
Artemisia tilhoana Quézel
Asplenium quezelii Tard.-Blot
Campanula bordesiana Maire*
C. monodiana Maire
Celsia tibestica Quézel
Ephedra tilhoana Maire
Eragrostis kohorica Quézel
E. monodii A. Camus
Foeniculum scoparium Quézel
Galium uniflorum Quézel
Helichrysum monodianum Quézel
Helosciadum muratianum Maire
Hyosciamus tibesticus Maire
Kosteletzkya borkouana Quézel
Lavandula antineae Maire
Lotus tibesticus Maire var. *tibesticus*
Nepeta mirei Quézel
N. tibestica Maire
* *Oldenlandia toussidana* Quézel
Pentas tibestica Quézel
Pentzia monodiana Maire
Potamogeton hoggariensis Dandy
Pulicaria volkonskyana Maire
Silene guichardi Chevassut et Quézel
S. mirei Chevassut et Quézel
S. toussidana Quézel
Stipa hoggariensis Chrtek et Martinovsky
Stipa tibestica Maire
Trigonella balachowskyi Leredde

Au total, 31 espèces, sauf omissions de notre part.

En attendant, des 'espèces endémiques strictes du Tibesti de souche montagnarde africaine' dont parle Quézel (1958) et alors au nombre de 10† il ne reste, d'après les recherches récentes, que *Pentas tibestica* non encore révisé et une espèce douteuse *Albuca septentrionalis.* Quant au *Ficus teloukat,* nous avons précisé en 1971, à son sujet (Lebrun & Peyr de Fabrègues, 1971): 'Selon Quézel, le *F. salicifolia* se différencierait notamment par ses fruits coriaces, alors qu'ils sont sucrés et comestibles chez *F. teloukat;* en fait, en herbier, les deux plantes paraissent très proches et nous ne les distinguerons pas.' Peut-être conviendra-t-il à la lueur de futures études, de considérer *F. teloukat* comme 'vicariant local et centro-saharien de *F. salicifolia*' comme l'écrit Quézel. En tous cas, le *F. salicifolia* est un bon exemple d'espèce d'Afrique nord-orientale et d'Arabie, présente dans les massifs sahariens. Finalement, le Tibesti est un point de rencontre de flores; ce qui est normal, vu sa place en Afrique; on y constate des espèces tropicales banales, des montagnardes africaines, des espèces méditerranéennes, des saharo-sindiennes, des soudano-zambéziennes. Mais l'endémisme propre au Tibesti, qu'il soit de souche tropicale ou de souche montagnarde africaine, que l'on a cru y voir, est quasi inexistant pour ne pas écrire nul.

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* Le genre *Amphinomia* est un synonyme de *Lotononis* (Rickett, 1960)

** Selon Thulin (1975) probablement conspécifique avec *C. edulis* Forsk.; mais le matériel vu par cet auteur était trop réduit pour effectuer la mise en synonymie.

† Quelques-unes ont été décrites depuis, telles *Agrostis tibestica, Festuca tibestica,* par exemple.

Mais après une telle hécatombe d'espèces 'nouvelles', une question vient immédiatement à l'esprit: reste-t-il encore quelque chose du cortège des endémiques des massifs sahariens? Nous pouvons répondre par l'affirmative.

3. *Endémiques vraies des massifs sahariens*

Elles appartiennent à des familles et à des genres très différents.

Actuellement, on en connaît 11, cartes en mains; de nouvelles études augmenteront peut-être très faiblement ce nombre; leur liste s'établit comme suit:

Bidens minuta
Centaurium flexuosum
Chiliadenus sericeus
Cupressus dupreziana
Erodium oreophilum
Fagonia tenuifolia
Myrtus nivellei
Salvia chudaei
Senecio hoggariensis
Solenostemma oleifolium
Lotus tibesticus

auxquelles on doit ajouter en second rang:

Olea laperrinei
Tripogon multiflorus

C'est à une connaissance insuffisante de la flore tropicale d'Afrique qu'est due la description de pseudo-espèces nouvelles; elle est le fait le plus souvent de botanistes spécialistes de la flore méditerranéenne.

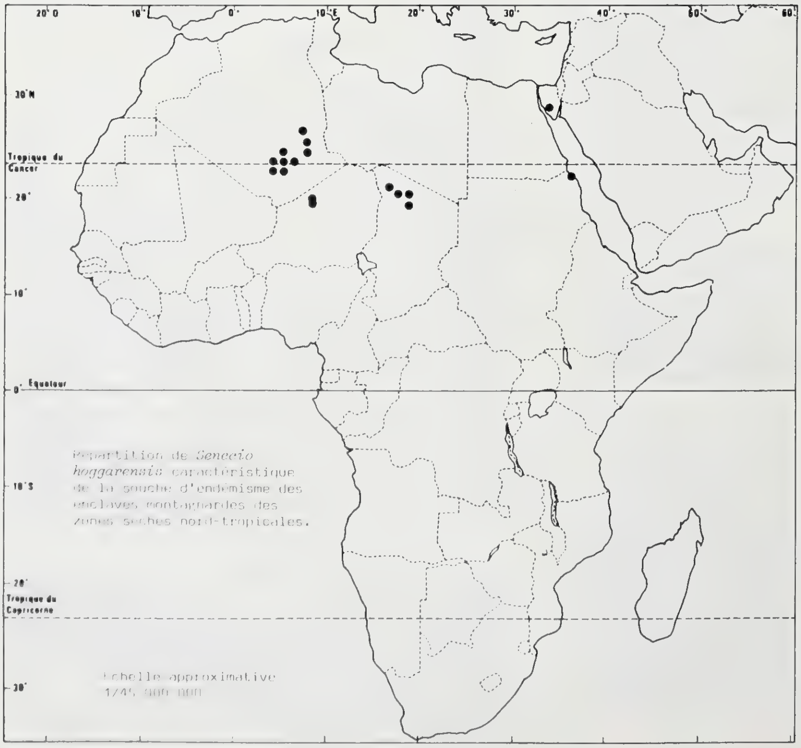
4. *La souche d'endémisme des enclaves montagnardes des zones sèches nord-tropicales*

Finalement, nous sommes tenté de créer, au sein de la souche d'endémisme saharo-sindienne, cette nouvelle entité, propre grosso modo à partir de 1 000 m d'altitude, aux massifs montagneux qui se dressent au Sahara, c'est-à-dire Hoggar, Tassili n'Ajjer, Aïr, Tibesti, Ennedi, Djebel Marra, Gebel Elba, avec, pour certaines espèces, possibilité d'extension à l'Arabie occidentale, au Sinaï et au NW de l'Afrique orientale.

En sachant fort bien que ces montagnes hébergent aussi des plantes présentes dans les montagnes de l'Afrique orientale, voire de l'Afrique du Sud et d'Angola (c'est le cas de *Rhynchosia totta* (Thunb.) DC. var. *venulosa* (Hiern) Verdc.) et que certaines espèces croissant dans des massifs sud-sahariens se retrouvent aussi en Arabie sud-occidentale (par exemple *Phagnalon scalarum* Schweinf. ex Schweinf.) tandis que *Senecio hoggarensis* Batt. et Tab. s'étend au Sinaï (Fig. 1).

Dès 1968, Gillet avait évoqué l'existence d'un endémisme au niveau des massifs sud-sahariens, mais limité à l'Aïr, au Tibesti et à l'Ennedi. Dix ans avant, Quézel (1958) estimait déjà que l'Aïr et le Tibesti justifiaient la création d'un sous-domaine spécial au sein du domaine érémitique africain septentrional.

Finalement, pour plus de détails sur les données fournies dans cet article, on consultera J.-P. Lebrun (1981).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Répartition de *Senecio hoggarensis* caractéristique de la souche d'endémisme des enclaves montagnardes des zones sèches nord-tropicales.
Echelle approximative 1/45 000 000

FIG. 1.—Répartition de *Senecio hoggarensis*, caractéristique de la souche d'endémisme des enclaves montagnardes des zones sèches nord-tropicales.

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Phytogeography of *Pelargonium*

J. J. A. VAN DER WALT* and P. J. VORSTER*

ABSTRACT

The vast majority of the approximately 200 species of *Pelargonium* occurs in Africa. About 80 per cent of the species are endemic to the winter rainfall region of the Cape Province, and the centre of distribution lies in the south-western Cape.

The distribution of the individual sections are discussed with the aid of distribution maps. The centre of distribution of most sections is in the south-western Cape, but a few sections are centred in the eastern and western Cape. Several sections are represented by a few species in the summer rainfall region of southern Africa.

As no fossils of *Pelargonium* are known, deductions about the origin of the genus can only be based on the present distribution of species, according to which arguments in favour of both a northern and a southern origin can be supported.

RÉSUMÉ

PHYTOGÉOGRAPHIE DES PELARGONIUM

La vaste majorité d'approximativement 200 espèces de Pelargonium *se trouve en Afrique. Environ 80% de ces espèces sont endémiques à la région à pluies d'hiver de la province du Cap et le centre de distribution est situé dans le Sud-Ouest du Cap.*

La distribution des sections individuelles est discutée à l'aide de cartes de distribution. Le centre de distribution de la plupart des sections est dans le Sud-Ouest du Cap, mais quelques sections sont centrées dans l'Est et l'Ouest du Cap. Plusieurs sections sont représentées par quelques espèces dans le région à pluies d'été de l'Afrique australe.

Comme aucun Pelargonium *fossile n'est connu, les déductions sur l'origine du genre peuvent seulement se baser sur la distribution actuelle des espèces, qui permet d'avancer des arguments en faveur d'une origine à la fois australe et nordique.*

INTRODUCTION

The genus *Pelargonium* was last revised by Knuth (1912) who recognized some 227 species which were accommodated in 15 sections. Knuth completely omitted *P. cotyledonis* (L.) L'Hérit. which we here place in a sixteenth and monotypic section, *Isopetalum* Sweet. Since 1912 a number of additional species have been described, but our revisionary work on the genus indicates that a number of species recognized by Knuth should be placed in synonymy (Van der Walt, 1977; Van der Walt & Vorster, 1981). On the other hand, a number of still undescribed species are known to us.

Goldblatt (1978) mentioned the Geraniaceae as one of the characteristic families of the Cape Floristic Region. This statement is based on the fact that the vast majority of *Pelargonium* species occur in the south-western Cape Province. Outside South Africa, the genus is represented by 18 species in the rest of Africa, eight in Australasia (Carolin, 1961; Swinbourne, 1970), two on Madagascar, two in Asia Minor and one each on the island of St Helena and Tristan de Cunha (Fig. 1).

The aim of the present paper is to present a global picture of the natural distribution of the genus and its sections. The survey is based on an intensive study of about 160 species occurring within the Flora of Southern Africa (FSA) region, whereas the distribution data for non-South African species were taken from herbarium specimens and literature.

DISTRIBUTION OF THE GENUS

The genus has a wide distribution practically throughout the FSA area (Fig. 2). However, by far the highest concentration of species is found in the south-western Cape Province, an area receiving winter rain. The one degree squares including the towns of Worcester and Cape Town have the highest concentration of species (Fig. 3.1). Fairly high concentrations of species are also found along the west coast extending to near the Orange River, and eastwards to the Cape/Transkei border. These areas receive rain either exclusively in winter or throughout the year.

The distribution of the genus coincides largely with that of Fynbos, but it can also be found in other vegetation types, such as grassland. Furthermore, although a high percentage of the species occurs in mountainous terrain on sandstone substrates, the genus is by no means confined to sandstone, and even geophytic representatives of the sections *Hoarea* (Sweet) DC. and *Seymouria* (Sweet) Harv. are sometimes found on heavy soils. On the whole, one of the most important factors determining the distribution of the genus probably is mild climatic conditions during the growing season. Generally the genus is absent in areas where the growing season is very hot. Over most of the distribution area, the plants are not subjected to temperatures far below freezing point during the growing season. In those parts of the distribution area where the summers become very hot or the winters very cold, the plants tend to die back and become dormant for the duration of the unfavourable season.

Although there is a dearth of information concerning the environmental conditions exper-

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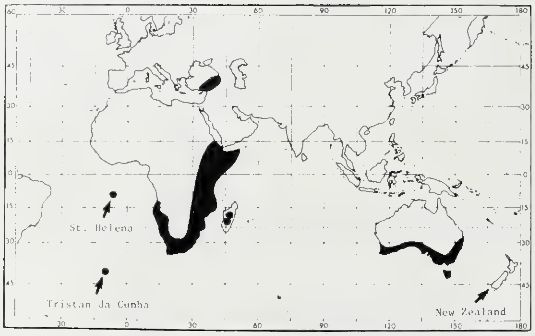

FIG. 1.—World distribution of the genus *Pelargonium*.

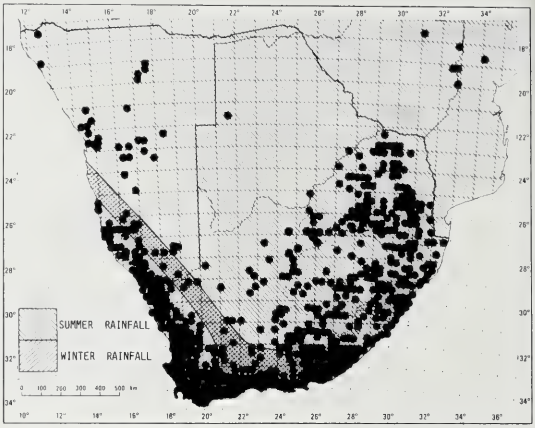

FIG. 2.—Distribution of the genus *Pelargonium* in the Flora of Southern Africa region.

ienced by the geographically more remote species, it is noteworthy that both the species in Asia Minor and Australasia occur between 30 and 40 degrees of latitude. The Australian species occur under climatic conditions not dissimilar to those reigning in the south-western Cape Province, and it is not unreasonable to accept that the basic environmental requirements of the genus are more or less similar for the majority of species. Apparently paradoxical is the occurrence of the genus in tropical east Africa, but it should be pointed out that these species are mostly associated with cool highlands which constitute a summer rainfall growing season climatically resembling the winter rainfall growing season experienced elsewhere.

DISTRIBUTION OF THE SECTIONS

The section *Pelargonium* is considered to be the most primitive section of the genus on account of its rather woody, much-branched, shrubby habit, simple leaves, and five-petalled flowers with seven fertile stamens. The 24 species occur in the south-western, southern and eastern Cape, extending northwards along the eastern escarpment (Fig. 3.2) to the eastern highlands of Zimbabwe. The two highest concentrations of species, in the south-western and southern Cape, fall entirely in the winter rainfall region. Many of them, however, do not occur in close association with Fynbos, but rather favour primitive, moist, shaded habitats, often in association with forest precursors. The species in the eastern Cape receive rain in winter as well as in summer, whereas those in the Transkei occur in a predominantly summer rainfall region. *P. graveolens* L'Hérit. extends through the summer rainfall area, from the eastern Cape to the eastern highlands of Zimbabwe (Müller, 1963), often in association with relic patches of high mountain Fynbos.

The section *Eumorpha* (Eckl. & Zeyh.) Harv. consists of subshrubs with only the bases of the stems woody. It is also considered to be a primitive section, because of its simple leaves and five-petalled flowers with mostly seven (rarely six) fertile stamens. Five of the eight species occur in the winter rainfall area with the highest concentration of species in the extreme south-western Cape Province. Of the species occurring outside the winter rainfall region, *P. transvaalense* Knuth is confined to a small area in the eastern Transvaal, whereas *P. alchemilloides* (L.) L'Hérit. occurs throughout the winter rainfall region and extends north-eastwards through the summer rainfall region (Fig. 3.3), possibly as far as Zimbabwe. In tropical east Africa (Kokwaro, 1971), the section is represented by two species.

The section *Ciconium* (Sweet) Harv. is also considered to be one of the primitive sections on account of the simple leaves and the almost regular five-petalled flowers. It does, however, exhibit certain advanced characters e.g. the herbaceous to semi-succulent stems of the subshrubs/shrubs, and in some species a reduced number of five fertile stamens. The sectional centre of distribution lies in the eastern Cape Province where three of the four species are concentrated, two of them endemic to that area. The third species, *P. zonale* (L.) L'Hérit., extends westwards far into the winter rainfall region, and a fourth species, *P. acraeum* R. A. Dyer, is endemic to the escarpment of Natal and the eastern Transvaal (Fig. 3.4). The eastern Cape populations get rain throughout the year, the Natal and Transvaal populations of *P. acraeum* summer rains, and *P. zonale* experiences winter rains where it intrudes into the winter rainfall area. The impression was gained that this is essentially not a winter rainfall section. *P. zonale*, the only species which occurs in both the summer and winter rainfall regions, is not plentiful in the winter rainfall region compared to its abundance further east where it experiences summer rain, and the species outside the purely winter rainfall area are usually not associated with Fynbos vegetation.

Although the section *Peristera* DC. consists of annuals or short-lived perrenial herbs, many species exhibit primitive characters such as simple leaves and rather regular five-petalled flowers with seven fertile stamens. Advanced characters such as a reduction of the number of petals and fertile stamens, are found in some representatives. In its present circumscription it includes a group of thirteen species in South Africa, extending northwards to the escarpment between Zimbabwe and Mozambique. It also includes one species in east

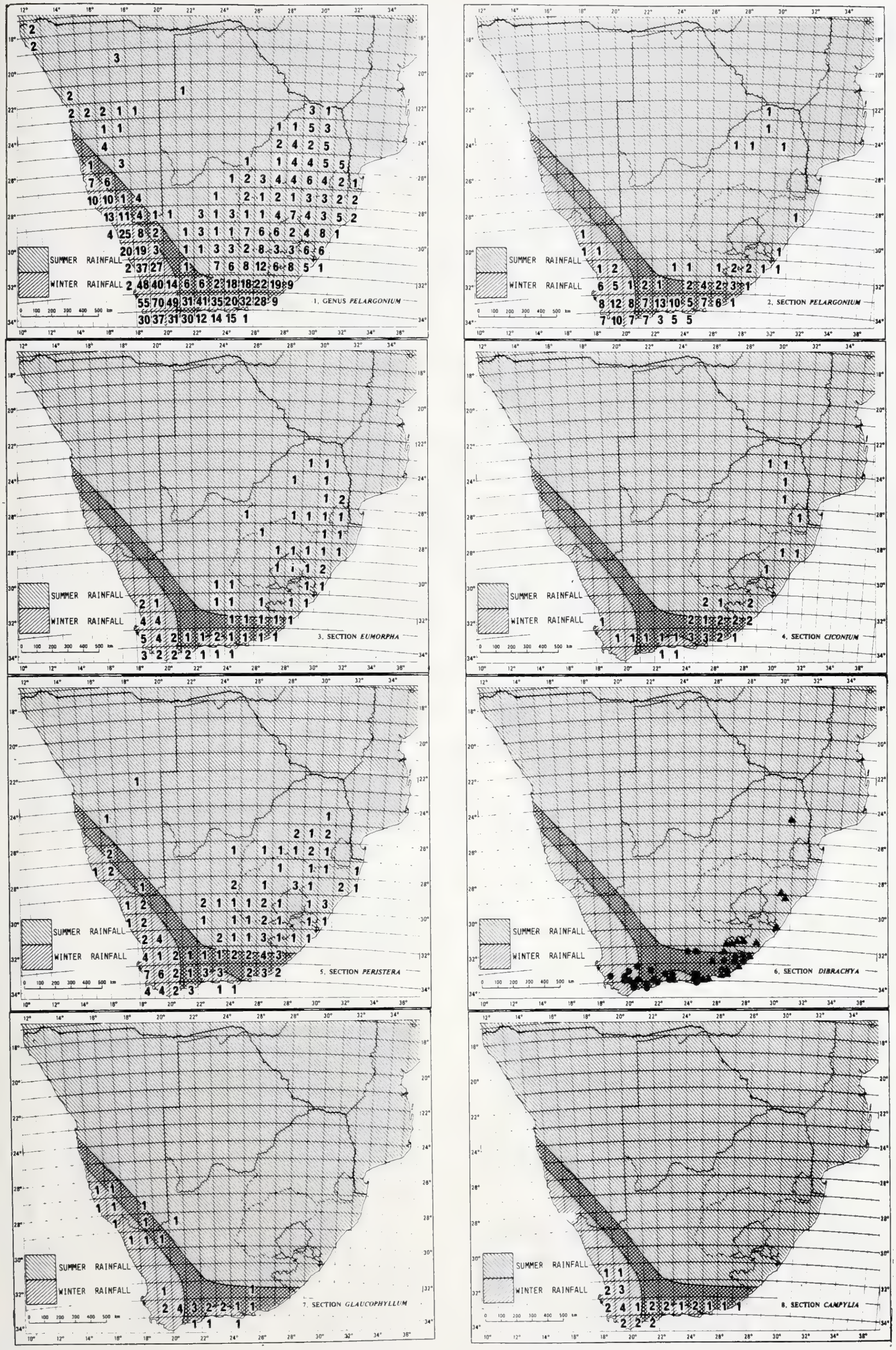

FIG. 3.—Distribution and concentration in the Flora of Southern Africa region of species of: 1, genus *Pelargonium;* 2, section *Pelargonium;* 3, section *Eumorpha;* 4, section *Ciconium;* 5, section *Peristera;* 6, section *Dibrachya* – ▲ *P. lateripes*, ● *P. peltatum;* 7, section *Glaucophyllum;* 8, section *Campylia.*

Africa, one or possibly two in Madagascar, one on the island of Tristan da Cunha and eight species in Australasia. It is possible that some of the non-South African species should be excluded from this section. The individual South African species tend to have surprisingly large distribution ranges, with at least half of them occurring in both the summer and winter rainfall areas. In South Africa the highest concentration of species occurs in the south-western Cape Province (Fig. 3.5). However, it is evident that the distribution of many species is not determined by either winter or summer rainfall. It is significant that several of the South African species have developed an annual habit to enable them to survive the dry season. As far as habitat preference is concerned, it is noteworthy that the non-South African species occur under conditions similar to those of the South African species.

The Section *Dibrachya* (Sweet) Harv. shows several advanced characters, such as a scrambling habit with relatively thin stems, somewhat succulent leaves, irregular flowers and often a reduced complement of fertile stamens. Primitive characters such as simple leaves and seven fertile stamens may indicate a relationship with the primitive section *Eumorpha*; in fact, a natural hybrid between these two sections has been reported. This section consists of two groups of populations, which may or may not be conspecific. The distribution of *P. peltatum* (L.) L'Hérit is very well correlated with the winter rainfall region of the south-western, southern and eastern Cape Province, although part of its range receives rain in summer as well. *P. lateripes* L'Hérit. occurs in the eastern Cape where its range overlaps with that of *P. peltatum*, and it is also found in the summer rainfall region of the Transkei, Natal and the eastern Transvaal (Fig. 3.6).

The section *Glaucophyllum* Harv. is advanced in respect of its herbaceous to semi-succulent stems, the unifoliolate or trifoliolate leaves, and reduced number of five fertile stamens in some species. However, the general floral structure (five petals) shows a link with the section *Pelargonium,* and this relationship is supported by the occurrence of natural hybrids between the two sections. This section of five species comprises a natural group of four species which occurs in low, dry shrubland from the eastern to the south-western Cape, within the winter rainfall region. The fifth species, *P. spinosum* Willd., is provisionally included in this section, but morphologically and phytogeographically it differs to such an extent from the mainstream of the section that it may be prudent to exclude it from this section altogether. It occurs in the north-western Cape Province and southern South West Africa on rocky outcrops under severely dry conditions (Fig. 3.7).

The section *Campylia* (Sweet) DC. consists of herbaceous subshrubs with simple leaves. There are four or five petals per flower, and the number of fertile stamens varies from five to seven. The nectar tube of the flower is usually shorter than the pedicel, in some species very short indeed. There is a remarkable resemblance between the flowers of certain species of the sections *Campylia* and *Pelargonium*, which may be indicative of a relationship between them. The distribution of the seven species of this section is well correlated with the winter rainfall region, with the highest concentration of species in the south-western Cape Province (Fig. 3.8). These plants have unswollen subterranean parts of considerable extent, often much more extensive than the exposed parts, which enable them to survive the hot and dry summers when the plants are dormant. This section is typically associated with low-lying, sandy flats.

The section *Otidia* (Lindl. ex Sweet) DC. consists of succulent subshrubs or shrubs with relatively thick branches. The rather regular flowers have five petals and five fertile stamens each. This section may be related to the monotypic section *Isopetalum* (Sweet) DC., which also has succulent stems and almost actinomorphic flowers. The seven species of the section *Otidia* occur within the winter rainfall region, with one species extending into the summer rainfall parts of the Cape Province. The largest concentration of species occurs along the western Cape coast (Fig. 4.1). These plants are well adapted to survive dry summers by virtue of their succulence and deciduous habit.

The section *Isopetalum* (Sweet) DC. consists of a single species, *P. cotyledonis* (L.) L'Hérit., a succulent subshrub with relatively thick branches and simple leaves. The flowers are regular with five petals, five or six fertile stamens, and a very short nectar tube. Its present very isolated geographical location on the island of St Helena (Fig. 1) does not appear to have great phytogeographical significance, but probably signifies that *P. cotyledonis* became isolated from the rest of the genus at an early stage and proceeded to adapt itself morphologically to the particular set of conditions reigning in its limited area of distribution, while at the same time retaining certain primitive characters which does not place it at a disadvantage where survival is concerned.

The section *Cortusina* (DC.) Harv. consists of subshrubs or shrubs, often with thick succulent branches, and simple leaves. The five-petalled flowers are rather regular, and there are six or seven fertile stamens. Similarities exist between the floral structure of the sections *Cortusina* and *Polyactium* DC., possibly indicating a relationship between the two sections. This affinity is supported by the presence of subterranean tubers in some species of *Cortusina.* The nine species of this section occur in southern S.W.A./Namibia, the western, south-western and eastern Cape Province, and thence northwards through the Orange Free State to the Transvaal (Fig. 4.2). Typically, the plants occur under rather dry conditions, which they survive by virtue of the succulence of the exposed and/or subterranean parts. The distribution of the section is to a considerable extent correlated with winter rainfall, although the centre of distribution lies in the eastern Cape in an area which in part receives rain throughout the year, and in part in summer only. Most species are rather restricted in their distribution, but there are two exceptions, namely *P. sidifolium* (Thunb.) Knuth and *P odoratissimum* (L.) L'Hérit., which extend into the summer rainfall region.

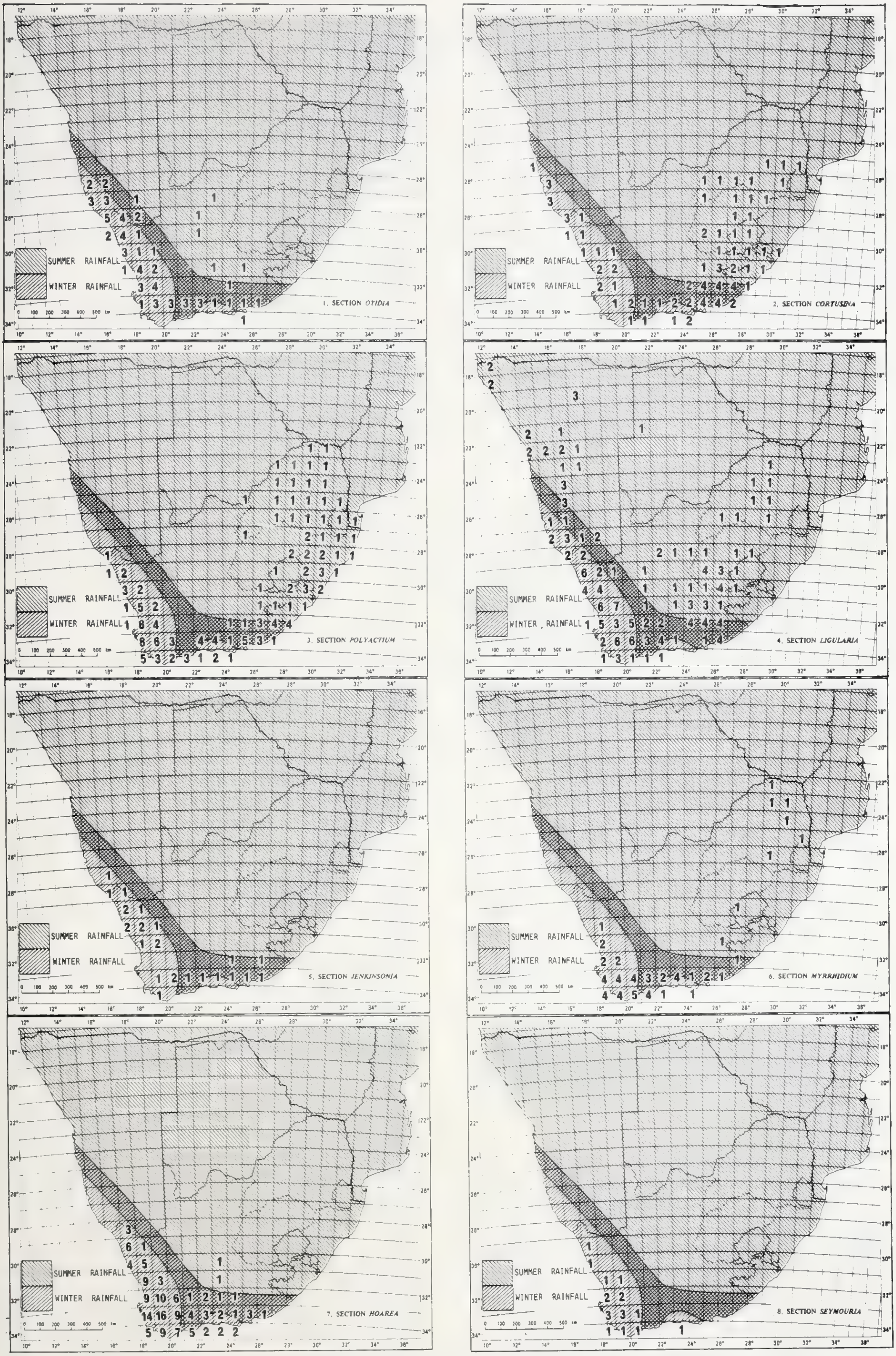

FIG. 4.—Distribution and concentration in the Flora of Southern Africa region of species of: 1, section *Otidia;* 2, section *Cortusina;* 3, section *Polyactium;* 4, section *Ligularia;* 5, section *Jenkinsonia;* 6, section *Myrrhidium;* 7, section *Hoarea;* 8, section *Seymouria.*

The section *Polyactium* DC. consists of geophytes with relatively large subterranean tubers. The leaves are simple to palmately or pinnately compound, radical and often heteroblastic. The flowers are rather regular with five petals and six or seven (exceptionally five) fertile stamens. Twelve of the thirteen species of this section are concentrated in a 200 km wide strip along the coast. To a large extent the distribution of these species are well correlated with the winter rainfall region. Two areas of concentration can be discerned, namely a major concentration in the south-western Cape Province and a secondary concentration in the eastern Cape. The abundance of species in the eastern Cape centre of distribution should be ascribed to the presence of an endemic eastern group, namely the *P. schizopetalum* Sweet — *P. caffrum* (Eckl. & Zeyh.) Harv. — *P. bowkeri* Harv. group. *P. luridum* (Andr.) Sweet has a very wide distribution and apart from a few scattered records from the southern Cape where it rains throughout the year, this is essentially a summer rainfall species (Fig. 4.3).

The section *Ligularia* (Eckl. & Zeyh.) Harv. comprises woody or herbaceous subshrubs with simple to compound leaves. The flowers have four to five petals each, and five or seven fertile stamens. The floral structure and vegetative characters suggest a relationship with the sections *Myrrhidium* DC. and *Jenkinsonia* (Sweet) DC. This section of about 27 species has a wide distribution throughout the FSA region (Fig. 4.4). Two definite areas of concentration can be discerned, namely in the south-western and western Cape Province where most species occur under winter rainfall conditions, and another in the eastern Cape Province under predominantly summer rainfall conditions.

The section *Jenkinsonia* (Sweet) DC. consists of woody, herbaceous or succulent subshrubs/shrubs with simple leaves. The inflorescences are borne on ordinary branches and consist of pseudo-umbels of one to five flowers each. The nectar tube of the flower is much longer than the pedicel. Each flower has four or five petals and seven fertile stamens. This section is most probably related to the sections *Myrrhidium* and *Ligularia*. The distribution area of the three species of the section *Jenkinsonia* is well correlated with the winter rainfall region of the Cape Province, although the eastern part of the range receives rain in summer as well. The species are usually found under rather dry conditions, where they form a component of low, dry shrubland (Fig. 4.5).

The section *Myrrhidium* DC. exhibits many advanced characters, namely herbaceous, trailing stems, compound leaves and a reduced number of four petals and five fertile stamens in several species. It shows a relationship to the sections *Ligularia* and *Jenkinsonia*. This section is also concentrated in the winter rainfall region where all five the presently recognized species occur, with the highest concentration in the Bredasdorp area. One species extends northwards along the eastern escarpment to the summer rainfall area through Natal and Transvaal (Fig. 4.6).

The sections *Hoarea* (Sweet) DC. and *Seymouria* (Sweet) Harv. are considered to be the most advanced sections because of their geophytic habit and the reduction of floral parts. In the section *Seymouria*, the number of petals is reduced to two, and in some species of the section *Hoarea* the number of fertile stamens is reduced to three or even two. These reductions result in pronouncedly zygomorphic flowers. Although the section *Hoarea* is the largest section in the genus, it has a rather limited distribution, coinciding almost entirely with the winter rainfall area of the south-western and western Cape Province, with only a few species present in the area which receives summer as well as winter rain. By far the highest concentration of species of the section *Hoarea* is known from the extreme south-western Cape (Fig. 4.7).

The section *Seymouria* is found in the south-western and western Cape Province under low winter rainfall conditions with the largest concentration of species in the south-west, but somewhat unexpectedly one population occurs near Knysna in the southern Cape under rather high rainfall conditions (Fig. 4.8). The plants of these sections are well equipped to survive the long, dry summer season by means of their underground tuberous parts.

DISCUSSION

The centre of distribution of most sections of *Pelargonium* is in the south-western Cape, but a few sections are centred in the eastern and western Cape. The following sections are clearly centred in the south-western Cape: *Eumorpha, Peristera, Campylia, Polyactium, Hoarea* and *Seymouria*. The sections *Ciconium* and *Cortusina* have their centres of distribution in the eastern Cape, whereas the sections *Otidia* and *Jenkinsonia* are centred in the western Cape. The sections *Pelargonium* and *Glaucophyllum* have centres of distribution in the south-western Cape as well as in the southern Cape, and *Ligularia* in the south-western and in the eastern Cape.

Several sections, though occurring mainly in the winter rainfall region, have one or more species extending through the summer rainfall region, e.g. the sections *Pelargonium, Eumorpha, Ligularia, Polyactium* and *Myrrhidium*. These species generally have a very wide distribution in the summer rainfall region. It is noteworthy that the section *Eumorpha,* which is considered to be one of the most primitive sections, is also represented in tropical east Africa, whereas the sections *Hoarea* and *Seymouria* which are considered to be the most advanced sections of the genus, are restricted to the winter rainfall region of the Cape Province.

As no fossil material of *Pelargonium* is known, deductions about the centre of origin of the genus can only be made on the present distribution of the species. The origin of the Cape Flora has always been a matter of controversy amongst botanists. There are followers of a temperate southern origin, and followers of a tropical origin. Willis (1922) theorized that the centre of variation of a genus coincides with the area of origin, and the very pronounced centre of variation of *Pelargonium* in the south-western Cape, tempts one to accept this as being also the centre of origin. White (1971) warned against the danger of adhering to such views, and pointed out that there had been so much climatic and physiographic change since the origin of many genera of flowering plants, that the phytochoria to which they belong would have been destroyed if they had not migrated, often for considerable distances. Support for a tropical origin of *Pelargonium* could be found in the fact that the presumed primitive sections are represented in tropical areas.

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Phytogeography of the tropical north-east African mountains

I. FRIIS*

ABSTRACT

The tropical north-east African mountains are tentatively divided into four phytochoria, the formal rank of which is not defined. The division is based on patterns of distribution and endemism in the region.

The recognition of a distinct Afromontane phytochorion is now well established (Chapman & White, 1970; Werger, 1978; White, 1978). However, there is still very little information on the phytogeography of the individual mountains or mountain systems. This study hopes to fill a little of the gap by analysing distribution patterns and patterns of endemism in the flora of the tropical north-east African mountains.

The north-east African mountain system is the largest in tropical Africa (see e.g. map in White, 1978). At the core of this system is the large Ethiopian massif, around which are located various mountains and mountain chains. These include the Red Sea Hills in the Sudan, the mountain chain in northern Somalia, the south-west Arabian mountains, and the Imatong mountains of south-east Sudan. The latter are often referred to the East African mountain system (White, 1978) but, as I will point out later, they also have a close connection with the south-west highlands of Ethiopia.

The paper presents some results of my study of the mountain flora of tropical north-east Africa, particularly the forest species. Where no source is indicated, the data are from my own unpublished studies.

RÉSUMÉ

LA PHYTOGÉOGRAPHIE DES MONTAGNES TROPICALES DE L'AFRIQUE DU NORD-EST

Les montagnes tropicales du nord-est africain sont divisées à titre d'essai en quatre phytochories, dont le rang n'est pas défini. La division est basée sur les modes de distribution et d'endémisme dans la région.

La reconnaissance d'une phytochorie afromontagnarde distincte est maintenant bien établie (Chapman & White, 1970; Werger, 1978; White, 1978). Cependant, il y a encore peu d'information sur la phytogéographie des montagnes individuelles ou des systèmes montagneux. Cette étude espère combler un peu cette lacune en analysant les modes de distribution et les modes d'endémisme dans la flore des montagnes tropicales du nord-est africain. Le système montagneux du nord-est africain est le plus grand de l'Afrique tropicale (voir carte dans White, 1978). Au coeur de ce système se trouve le grand massif éthiopien autour duquel sont situées des montagnes et des chaînes de montagnes variées. Celles-ci incluent les collines de la Mer Rouge au Soudan, la chaîne de montagnes de la Somalie du Nord, les montagnes du Sud-Ouest de l'Arabie et les montagnes Imatong du Sud-Est du Soudan. Ces dernières sont souvent mentionnées comme système montagneux de l'Est africain (White, 1978) mais comme je le soulignerai plus tard, elles ont aussi une étroite connection avec les hauts plateaux du Sud-Oust de l'Ethiopie.

Le document présente certains résultats de mon étude de la flore de montagne du Nord-Est tropical de l'Afrique, particulièrement les espèces forestières. Là où aucune source n'est indiquée, les données proviennent de mes propres études non encore publiées.

PATTERNS OF ENDEMISM

The endemism of the tropical north-east African mountains can be divided into four geographical groups:

1. *Endemics of the south-western part of the Ethiopian highlands.*

The species in this group are associated with upland rain forest or humid evergreen bushland, and include:

Aframomum korarima (Pereira) Engl.	Fig. 1.
Amorphophallus gambozianus Pich.-Serm.	Same as Fig. 1.
Cirsium englerianum O. Hoffm.	Fig. 2; Friis, 1975.
Cirsium dender Friis	Fig. 2; Friis, 1975.
Diaphananthe adoxa Rasm.	Rasmussen, 1974.
Dorstenia soerensenii Friis	Friis, 1974.
Polystachya aethiopica Cribb	Fig. 3; Cribb, 1978; own data.
Scadoxus nutans (Friis & Bjørnst.) Friis & Nordal	Friis & Bjørnstad, 1971.
Streptocarpus phaeotrichus B. L. Burtt	Fig. 4; Hilliard & Burtt, 1971; own data.
Tiliachora troupinii Cuf.	Fig. 5; Benvenuto, 1975; own data.

An interesting group of endemics, which is recognized here for the first time, is restricted to south-western Ethiopia and the Imatong mountains. Examples are:

Bidens imatongensis Sherff	Fig. 6.
Guizotia arborescens Friis	Friis, 1971.
Impatiens ethiopica Grey-Wilson	Fig. 7; Grey-Wilson, 1980; own data.
Senecio myriocephalus A. Rich.	Fig. 8.

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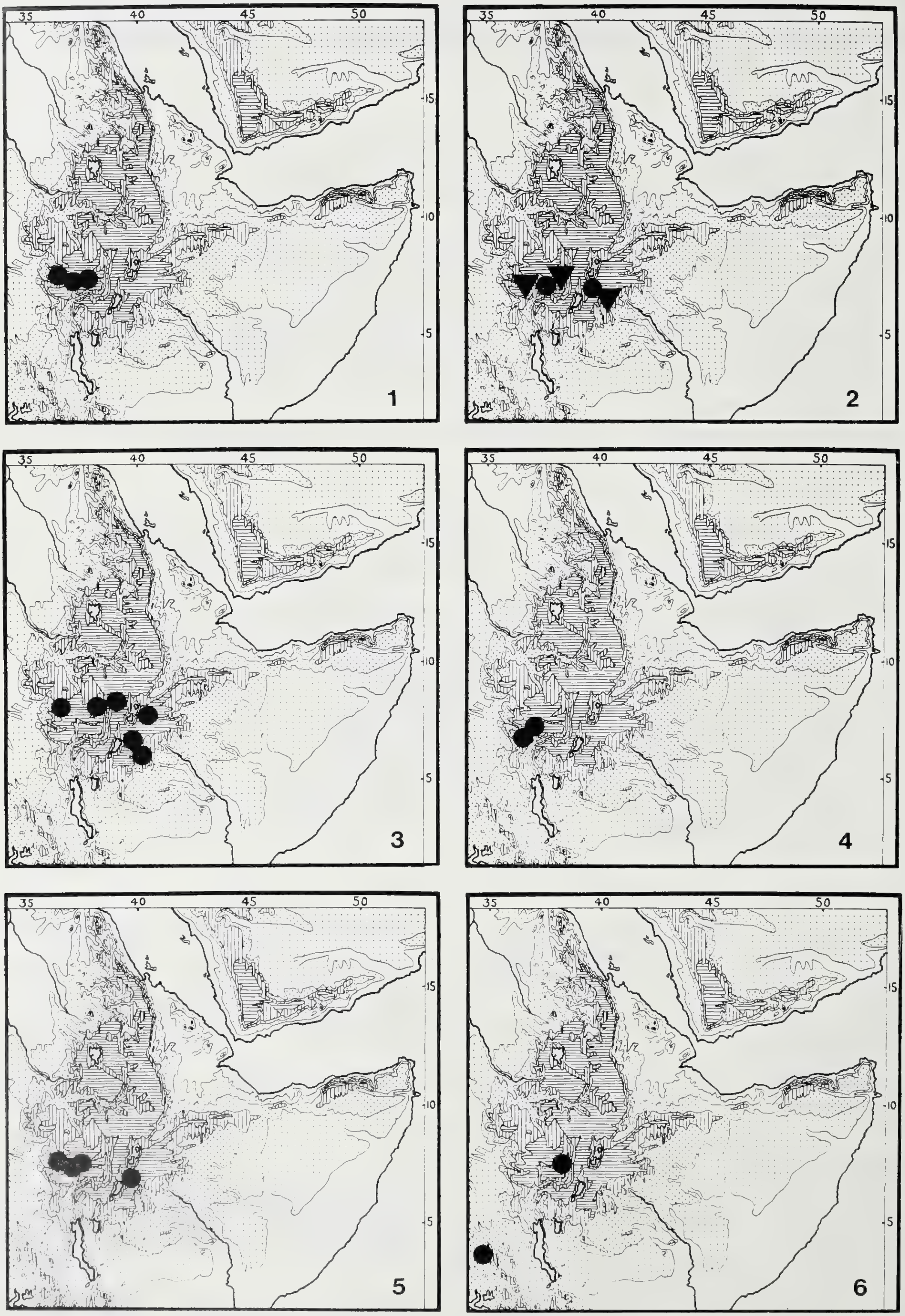


FIGS 1–6.—Distribution of: 1, *Aframomum korarima* (Pereira) Engl. (c. 1 700–c. 2 000 m); 2, *Cirsium englerianum* O. Hoffm. (dots, 1 750–2 100 m), *Cirsium dender* Friis (triangles, 2 300–2 500 m); 3, *Polystachya aethiopica* Cribb (1 350–2 500 m); 4, *Streptocarpus phaeotrichus* B. L. Burtt (c. 1 600–1 800 m); 5, *Tiliachora troupinii* Cuf. (1 700–1 900 m); 6, *Bidens imatongensis* Sherff (1 700–2 300 m). The hatching on this and the following maps signifies: no hatching — under 500 m; open dots — 500–1 000 m; closed dots — 1 000–1 500 m; vertical hatching — 1 500–2 000 m; horizontal hatching — over 2 000 m.

Other connections exist, for example:

Coffea arabica L. South-west Ethiopia, Imatong Mountains and Mt Marsabit.	Friis, 1979; own recent data.

2. *Endemics of the high mountains of Ethiopia*

Species in this group occur mainly in ericaceous bushland or in afro-alpine vegetation types. Examples are:

Jasminum stans Pax	Fig. 9.
Rosularia semiensis (A. Rich.) H. Ohba	Fig. 10.
Hypagophytum abyssinicum (Hochst.) Berger. Monotypic genus.	Fig. 10.
Saxifraga hederifolia A. Rich.	Rampi, 1973.
Philippia abyssinica Pich.-Serm. & Hein	Pichi-Sermolli & Heiniger, 1953.
Lobelia rhynchopetalum (A. Rich.) Hemsl.	Fig. 11.

A few endemics on the high mountains are found also on one other isolated mountain, for example:

Blaeria spicata A. Rich. Also on Jebel Marra.	Pichi-Sermolli & Heiniger, 1953.

3. *Endemics of the Ethiopian plateau*

Species in this group seem to be confined to the plateau of northern and central Ethiopia, and occur in comparatively dry vegetation types, e.g. on slopes, rocky outcrops and stony, well-drained soil. Examples are comparatively few when compared with other groups:

Cussonia ostinii Chiov.	Bamps, 1974.
Polyscias farinosa (Del.) Harms	Bamps, 1974.

4. *Endemics of the eastern escarpment of the Ethiopian plateau and associated mountains.*

Species in this group are more or less confined to the eastern escarpment of the Ethiopian plateau, the mountain chain in northern Somalia, and the south-west Arabian mountains. Some species in this group may also occur on Socotra and on Jebel Akhdar in Oman. The species occur in upland dry evergreen forest or in associated types of evergreen bushland. (These endemics should not be confused with the even more important group of endemics in the deciduous bushlands of the Ogaden and the Somalian lowlands.) The most notable example in this group is *Barbeya oleoides* Schweinf., representing a monotypic family (Fig. 12). Other examples are:

Mimusops laurifolia (Forssk.) Friis	Fig. 13; Friis, 1981.
Buxus hildebrandtii Baill.	Valenti, 1965.
Spiniluma oxyacantha (Baill.) Aubrev. Also penetrates the drier parts of the plateau; replaced on Socotra by the very closely related *S. discolor* (Radcliffe-Smith) Friis.	Fig. 14; Friis, 1978.
Poskea Vatke. Endemic genus; three species in north-east Somalia, one also on Socotra	Morucchio, 1970

DISTRIBUTION OF NON-ENDEMICS

Non-endemics show patterns of distribution similar to the grouping of the endemics outlined above. Most notable are the south-western species and the species of the eastern Ethiopian escarpment.

1. *South-western species*

Examples of this group are:

Morus mesozygia Stapf. Widespread in tropical Africa.	Fig. 20
Trichilia dregeana Sond. Also East and South Africa.	Wilde, 1968.

2. *Species of the Ethiopian high mountains*

Examples are:

Subularia monticola Schweinf.	Hedberg, 1962.
Ranunculus oreophytus Del.	Hedberg, 1962.

Both species occur on the high mountains of East Africa.

3. *Species of the Ethiopian plateau*

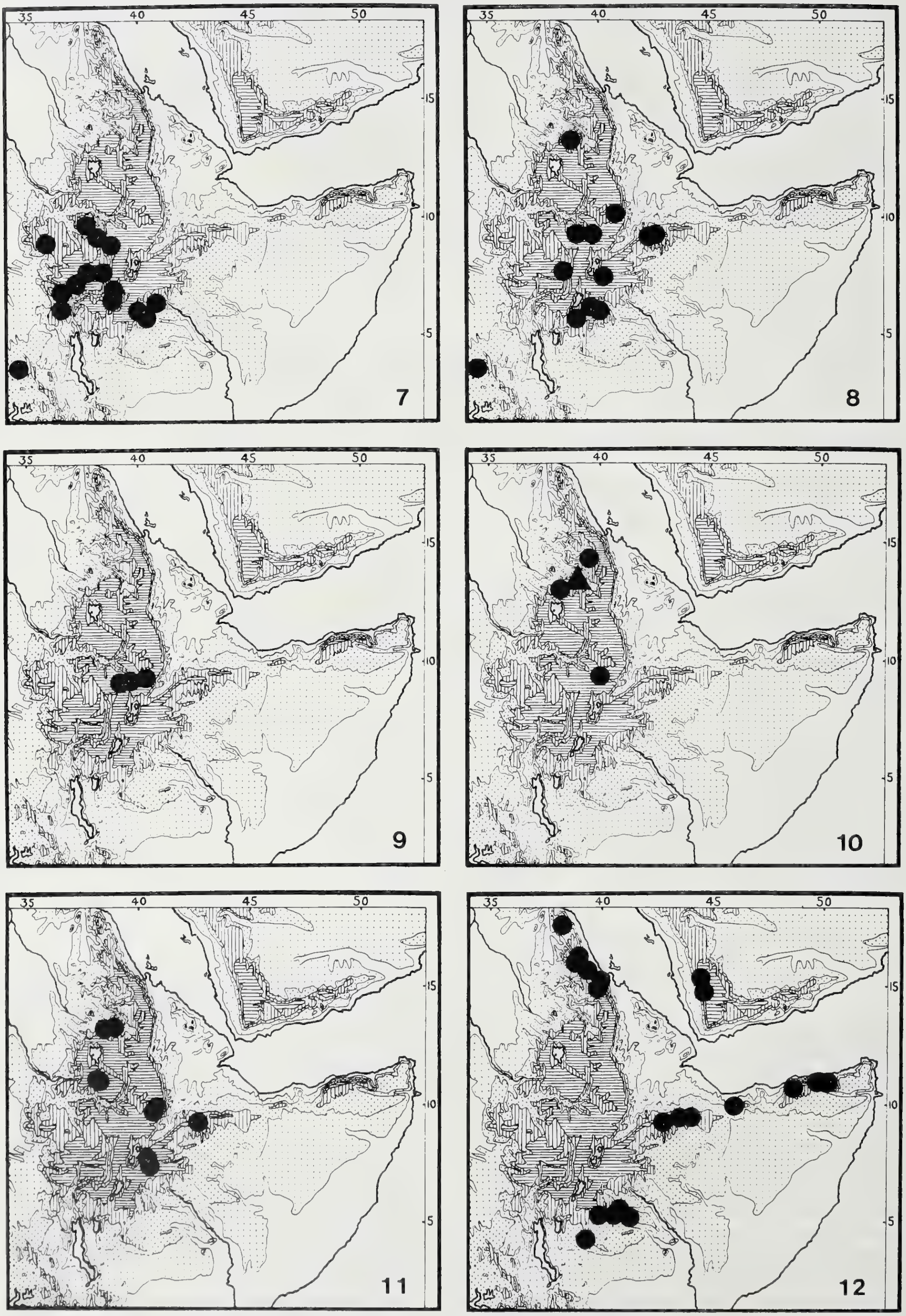
Examples of this distribution may be found in the genus *Acacia*, but the taxonomy and distribution of the species of this genus in Ethiopia have not yet been published.

A. pilispina Pich.-Serm. may be a good example (Ross, 1979).

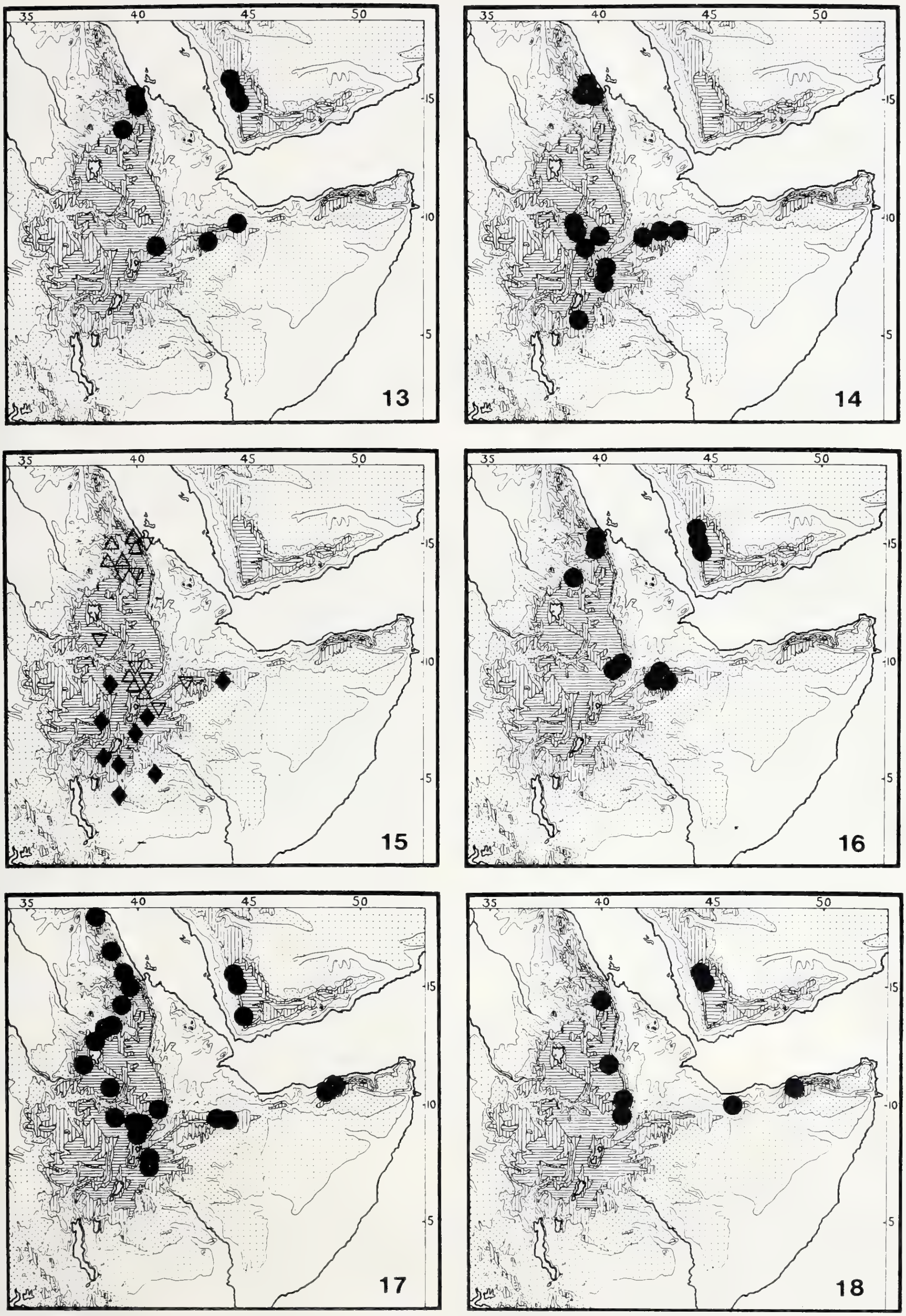
4. *Species of the eastern Ethiopian escarpment and adjacent mountains*

Examples are:

Berberis holstii Engl. Closely related to the Himalayan *B. aristata* DC., also in the south-western Arabian mountains and East Africa.	Fig. 18; Polhill, 1966.
Pistacia aethiopica Kokwaro. Related to the Mediterranean *P. lentiscus* L., also in East Africa.	Fig. 19; Kokwaro & Gillett, 1980.



FIGS 7–12.—Distribution of: *Impatiens ethiopica* Grey-Wilson (1 300–3 200 m); 8, *Senecio myriocephalus* A. Rich. (c. 2 500–c. 3 100 m); 9, *Jasminum stans* Pax (c. 3 000 m); 10, *Rosularia semiensis* (A. Rich.) H. Ohba (triangle, above 3 000 m) and *Hypagophytum abyssinicum* (A. Rich.) Berger (dots, also on same locality as *R. semiensis*, above c. 2 700 m); 11, *Lobelia rhynchopetalum* (A. Rich.) Hemsl. (2 790–4 080 m); 12, *Barbeya oleoides* Schweinf. (1 300–2 500 m).



FIGS 13–18.—Distribution of: 13, *Mimusops laurifolia* (Forssk.) Friis (500–1 800 m); 14, *Spiniluma oxyacantha* (Baill.) Aubrév. (1 800–2 800 m); 15, *Linum trigynum* L. (triangles pointing S, 2 000–2 750 m), *Linum corymbulosum* Reichb. f. (triangles pointing N, c. 1 000–c. 2 500 m), *Linum volkensii* Engl. (rhombi, 1 600–2 800 m); 16, *Debregeasia bicolor* (Roxb.) Wedd. (1 500–2 400 m); 17, *Rosa abyssinica* Lindl. (c. 2 500 m to above 3 000 m); 18. *Berberis holstii* Engl. (1 500–3 200 m).

Juniperus procera Endl. Penetrates the drier parts of the plateau; also in the south-west Arabian mountains and East Africa.	Fig. 21.
Tarchonanthus camphoratus L. Also in the south-west Arabian mountains and in East and South Africa.	Fig. 22.
Monotheca buxifolia (Falconer) A. DC. Also on Jebel Akhdar in Oman and in north-east Afghanistan and adjacent parts of Pakistan.	Fig. 23; Friis, 1978.
Ceratonia oreothauma Hillc., Lewis & Verdc. Also in Oman.	Hillcoat, Lewis & Verdcourt, 1980.

VICARIISM

It has been suggested that vicariism is extremely important in the Afromontane flora, and that species replace each other on different mountains. White, on the other hand, concludes (Chapman & White, 1970), from his analysis of the Afromontane tree flora of Malawi, that vicariism scarcely exists in that area.

A moderate degree of vicariism seems to exist between the Afromontane flora of tropical north-east Africa and that of other Afromontane areas. Of the endemics mentioned, only the following are not replaced by vicarious species either in the Mediterranean or temperate regions or on other African mountains:

Endemic genera: *Hypagophytum, Spiniluma,*

Barbeya and *Poskea.* Endemic section:

Scadoxus sect. *Gamolepis;* only species, *S. nutans.*

A case of local vicariism is found in *Linum* L.: the Mediterranean species *L. strictum* L. and *L. corymbulosum* Reichb. f. occur in northern and central Ethiopia, but seem in southern Ethiopia to be replaced by the Afromontane endemic *L. volkensii* Engl., which also occurs in East Africa (Fig. 15).

OUTLIERS

According to Gillett (1955) the flora of three vegetation types in south Ethiopia is more closely related to the flora of the East African mountains than to the flora of northern Ethiopia. It would appear from this that elements of the northern and southern floras of Ethiopia might have a closer affinity to the floras to the north and south of them respectively. That this is correct, at least to some degree, is shown by a number of species or genera which reach their southernmost limit in Ethiopia and Somalia, but which occupy their main range in the temperate or Mediterranean areas, or in the Himalayas. Similarly, there are a number of species and genera which reach their northernmost limit in Ethiopia.

1. *Southern limit species*

Examples are:

Rosularia (DC.) Stapf. c. 25 species; distributed from the eastern Mediterranean to central Asia. The only African species is *R. semiensis* (Fig. 10), which reaches its southern limit in the Semien mountains.

Saxifraga L. c. 300 species; occurring in the temperate region and in the Himalayas. The only African species, *S. hederifolia,* reaches its southern limit in the Arussi mountains (Rampi, 1973).

Debregeasia Gaud. c. 17 species; a genus of tropical and subtropical Asia, with many species in the Himalayas. The only African species, *D. bicolor* (Roxb.) Wedd., is distributed from the western Himalayas to Harar and Shoa (Fig. 16).

Rosa L. c. 150 species; a widespread genus in the north temperate area. Only one African species, *R. abyssinica* Lindl., which is closely related to the *R. moschata* group of the Himalayas and western China. It occurs in the Yemen and Ethiopia as far south as Bale (Fig. 17).

Primula L. c. 500 species; a widespread genus in the north temperate region and the Himalayas. The only African species, *P. verticillata* Forssk. occurs in the south-west Arabian mountains and in Ethiopia, with a southern limit just south of Addis Ababa (Bizzari, 1970).

2. *Northern limit species*

There is a large number of southern Afromontane genera and species which reach their northern limit in Ethiopia and Somalia. A few examples taken from the Afromontane shrubs and trees are:

Schefflera J. R. & G. Forster. Three species of this genus are important in the forests of Ethiopia. Two of them, *S. volkensii* (Engl.) Harms and *S. myriantha* (Bak.) Drake, reach their northern limit at the latitude of Addis Ababa. The third species, *S. abyssinica* (A. Rich.) Harms, has its northern limit in Tigre (Bamps, 1974).

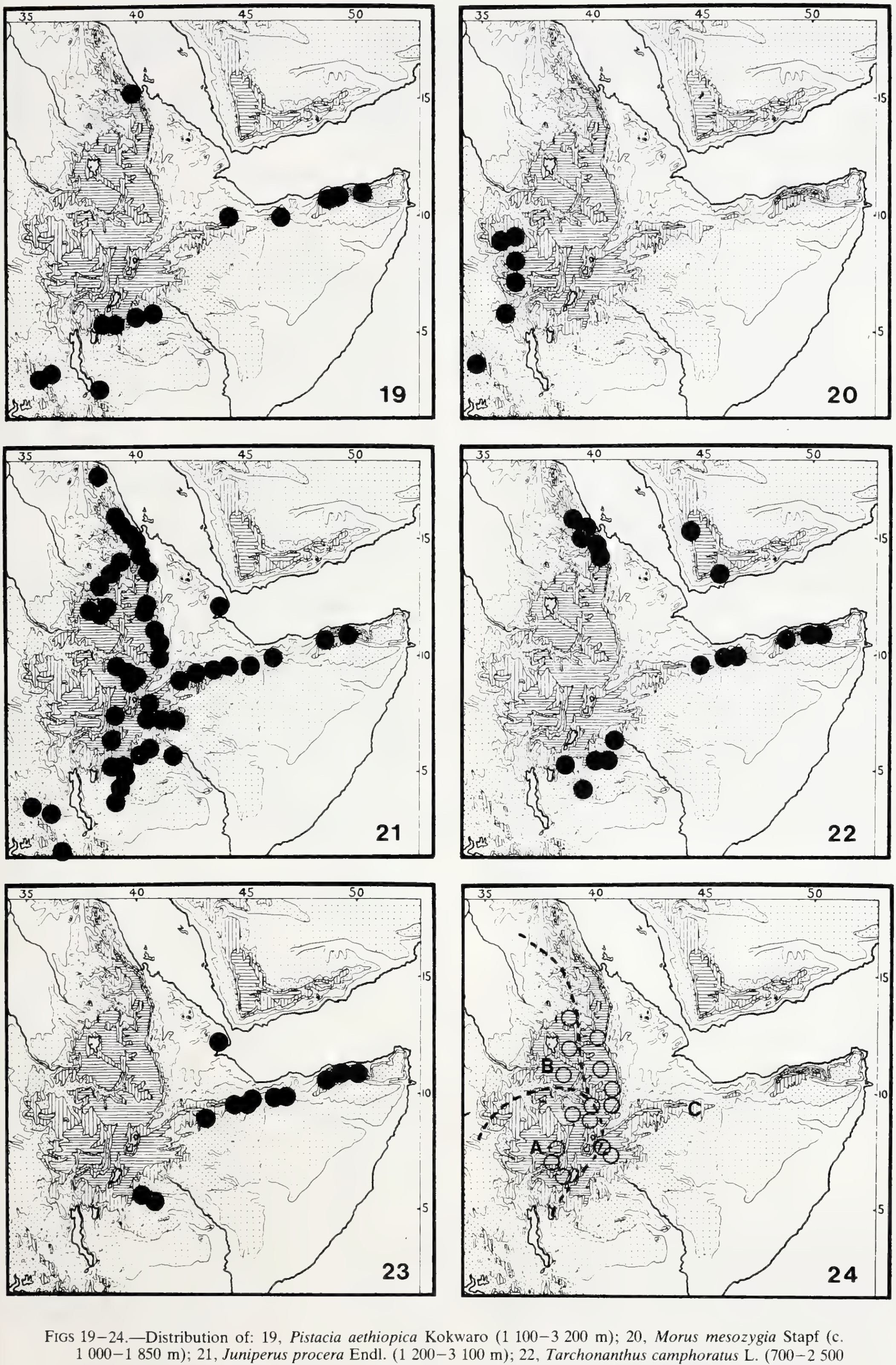
Psychotria orophila Petit. A common forest species with the same northern limit as *Schefflera volkensii* and *S. myriantha* (Petit, 1972).

Hypericum L. Examples similar to those of *Schefflera* can be found among the woody species of *Hypericum* (Bamps, 1971).

CONCLUSION

As seen from the distribution maps and data presented above, there seems to be reasonably good coincidence between the patterns of distribution revealed. It is therefore tempting to suggest that these patterns represent some kind of division of the tropical north-east African mountains into four phytochoria (Fig. 24).

Classical hierarchical biogeographical classifications have been less widely accepted in the recent years. White (1978) now prefers a less formal system of centres of endemism and transition zones and regional mosaics, rather than classifying the phyto-



FIGS 19–24.—Distribution of: 19, *Pistacia aethiopica* Kokwaro (1 100–3 200 m); 20, *Morus mesozygia* Stapf (c. 1 000–1 850 m); 21, *Juniperus procera* Endl. (1 200–3 100 m); 22, *Tarchonanthus camphoratus* L. (700–2 500 m); 23, *Monotheca buxifolia* (Falconer) A. DC. (1 250–2 150 m); 24, A tentative phytogeographical division of the tropical N. E. African highlands: A, south-western endemics and many southern Afromontane species; B, plateau endemics and some northern and southern species; C, eastern endemics and many northern and southern species; open dots, high altitude endemics and both northern and southern species.

choria in provinces, regions and domains. I tentatively suggest that the four phytochoria on Fig. 24 represent four local centres of endemism. with the Ethiopian plateau as the least marked one.

Croizat, Nelson & Rosen (1974) have suggested the term 'generalized track' for persistently repeated distribution patterns. Tracks indicated by a fraction of the total number of species are termed 'coincident individual tracks'. As seen from the data presented for non-endemics and outliers, the four phytochoria on Fig. 24 can also be taken to represent such coincident individual tracks.

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Contribution à l'étude des lichens du Kivu (Zaïre), du Rwanda et du Burundi. VII. Approche écogéographique de la flore et de la végétation lichéniques dans l'est de l'Afrique centrale

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RÉSUMÉ

Un historique est esquissé de l'exploration lichénologique de l'Afrique intertropicale, plus particulièrement du territoire formé par le Kivu (Zaïre), le Rwanda et le Burundi; il comporte un bilan sommaire du matériel récolté et de l'état d'avancement de son étude taxonomique. Une analyse des éléments phytogéographiques présents dans la dition permet de distinguer les catégories suivantes (certaines avec des variantes significatives): subcosmopolite, tempéré-tropical, pantropical, paléotropical, afro-néotropical, guinéo-congolais, soudano-zambésien, zambésien-afrooriental et zambésien, endémique de la région des lacs centrafricains, afromontagnard et afroalpin. Enfin un premier aperçu est donné des types de répartition des lichens dans la dition et de la place occupée par ces organismes dans les principaux paysages végétaux de celle-ci.

ABSTRACT

A short historical record of the lichenological exploration of tropical Africa, especially Kivu (Zaïre), Rwanda and Burundi is given, including an account of the material collected and of the present state of taxonomic knowledge of the lichens. Several phytogeographical categories can be recognized in this area; they are (some with significant variants): subcosmopolitan, temperate-tropical, pantropical, paleotropical, afro-neotropical, guineo-congolian, sudano-zambezian, zambezian-afrooriental and zambezian, central African lakes endemic, afromontane and afroalpine. The distributional types of the lichens within the studied area are briefly described, as well as their importance in the main vegetation types.

1. HISTORIQUE

L'exploration lichénologique de l'Afrique intertropicale a débuté à la fin du 19e siècle, mais, jusqu'à ces dix dernières années, elle est restée sporadique et fragmentaire. Les premières publications ne sont guère que des inventaires de récoltes occasionnelles, effectuées par des personnes étrangères à la lichénologie, voire à la botanique, lors de missions de prospection biologique et autre; ou alors il s'agit de la description de telle ou telle espèce nouvelle dans des travaux généraux sur les lichens tropicaux, tels que ceux de Hue, Zahlbruckner, etc . . . Un premier catalogue bibliographique de la 'Lichenaea Africana' est celui de Stizenberger (1890, 1891, 1893, 1895). Plus récemment, on ne peut passer sous silence la flore entreprise par Dodge (1953, 1956, 1957, 1959, 1964, 1971), mais celle-ci est malheureusement pratiquement sans valeur et elle encombre malencontreusement la littérature, surtout d'un point de vue nomenclatural. Pour un aperçu des publications utilisables en pratique pour l'étude de ces lichens, on consultera plus particulièrement la synthèse bibliographique de Hawksworth (1977). Parmi les données récentes, il convient d'épingler les nombreux travaux, d'un intérêt exceptionnel, consacrés depuis 1974 par Krog & Swinscow (1974, 1975a & b, 1976, 1977, 1979, 1981) et Swinscow & Krog (1974, 1975a, b, c & d, 1976a, b, c & d, 1978a & b, 1979a & b, 1981) essentiellement aux macrolichens d'Afrique orientale, ainsi que les publications de Vězda sur les lichens foliicoles (en particulier 1975 & 1980) et les Asterothyriaceae (1979).

En ce qui concerne l'est de l'Afrique centrale, plus précisément la région formée par le Kivu (Zaïre), le Rwanda et le Burundi, l'exploration lichénologique s'était pratiquement limitée jusqu'à ces dernières années aux portions montagneuses de cette zone de grandes fractures tectoniques, où se manifestent aussi d'importants phénomènes volcaniques. C'est le Ruwenzori qui fut le plus anciennement et le plus souvent parcouru, bien que les collections rassemblées ne donnent manifestement qu'un médiocre reflet de la richesse de la flore lichénique du massif. Citons les récoltes des expéditions de G.F. Scott-Elliot (Vainio, 1898), du duc des Abruzzes (Jatta, 1908), de L. Hauman (Zahlbruckner & Hauman, 1936) et de H. Humbert (des Abbayes, 1941). Humbert parcourut également la chaîne des volcans Birunga et le massif du Kahuzi-Biega, explorés par ailleurs par H.V. Stauffer en 1954–55 (Motyka, 1959; des Abbayes, 1962; Frey, 1967). Enfin, on mentionnera les quelques récoltes faites au début du siècle par l'expédition allemande de J. Mildbraed, notamment dans la forêt de Rugege au Rwanda (Lindau, 1911) et par celle d' 'Exploration hydrobiologique du lac Tanganika' (des Abbayes, 1958).

2. EXPLORATION ET ÉTUDES RÉCENTES

L'Afrique orientale (Ethiopie, Kenya, Uganda, Tanzanie) a fait l'objet depuis une dizaine d'années d'une prospection lichénologique importante, surtout de la part de H. Krog, de T.D.V. Swinscow et de T. Pócs. Les matériaux recueillis sont en cours d'étude, en même temps que des collections quelque peu antérieures rassemblées principalement par R.A. Maas Geesteranus, R. Santesson et O. Hedberg.

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En ce qui concerne le Zaïre, le Rwanda et le Burundi, des récoltes ont été faites depuis une cinquantaine d'années par les botanistes belges, mais elles ne concernent guère que des lichens ayant une importance physionomique marquée dans le paysage végétal; elles sont conservées essentiellement à BR, BRVU, BRLU et LG. Elles n'avaient été que peu étudiées jusqu'ici.

L'est de cette région, plus précisément le Rwanda et le Burundi et certaines portions du Kivu (principalement le Kahuzi-Biega, les Birunga centraux et orientaux, et dans une moindre mesure la plaine de lave de Goma, la plaine de la Rwindi-Rutshuru et la forêt équatoriale d'Irangi), a fait l'objet de récoltes intensives de la part de l'un de nous (J.L.) au cours de plusieurs missions depuis décembre 1971. Quelque 3 000 lichens ont été ainsi rassemblés. Une présentation écogéographique de cette dition a été faite par Lambinon & Sérusiaux (1977).

L'étude du matériel recueilli a été poursuivie depuis cette époque, avec en priorité les lichens foliicoles et les macrolichens. Ont été publiées jusqu'ici les données relatives aux genres suivants: *Everniopsis, Normandina* et *Placopsis* (Lambinon & Sérusiaux, 1977), *Stereocaulon* (Sérusiaux, 1979b), *Leprocaulon* (Lambinon, Ramaut & Sérusiaux, 1981) ainsi que *Coccocarpia* et *Lobaria* (Sérusiaux, 1981); il en va de même de quelques groupes de foliicoles (Sérusiaux, 1978 et 1979a) et des Caliciaceae (Tibell, 1981); à noter que le genre *Stereocaulon,* particulièrement bien représenté dans la dition, avait antérieurement fait l'objet d'une étude descriptive méritoire de Duvigneaud (1956). D'autres groupes sont à l'étude, menée partiellement en collaboration avec divers spécialistes; outre les épiphylles, citons notamment les Gyalectaceae sensu Zahlbruckner (A. Vězda), les Pannariaceae (P.M. Jørgensen), les genres *Erioderma* et *Nephroma* (G. Keuck), les *Xanthoria* et *Teloschistes* (O. Almborn), les *Parmelia* s.l., les *Ramalina,* diverses Physciaceae et Cladoniaceae, . . .

3. ELÉMENTS PHYTOGÉOGRAPHIQUES

Le classement des représentants d'un groupe taxonomique déterminé dans un territoire donné en une série d'éléments phytogéographiques est toujours matière à discussion, ce qui résulte d'abord de l'inévitable schématisation qu'implique le regroupement des multiples types de répartition en un nombre limité de catégories. En plus, dans le cas des lichens, comme de beaucoup de cryptogames d'ailleurs, même si la taxonomie du groupe est bien établie, l'information chorologique reste fragmentaire pour bien des régions intertropicales, souvent encore mal prospectées. Le 'survey' tenté ci-après des éléments reconnus dans la dition ne constitue donc qu'une première tentative de synthèse phytogéographique de sa flore lichénique.

(a) *Elément subcosmopolite*

C'est le cas, manifestement très rare, de taxons très largement répandus sur tous les continents, même si de grandes lacunes (réelles ou en partie dues à un manque d'information) peuvent subsister. Ex.: *Candelaria concolor* (Dicks.) Stein et *Chrysothrix candelaris* (L.) Laundon.

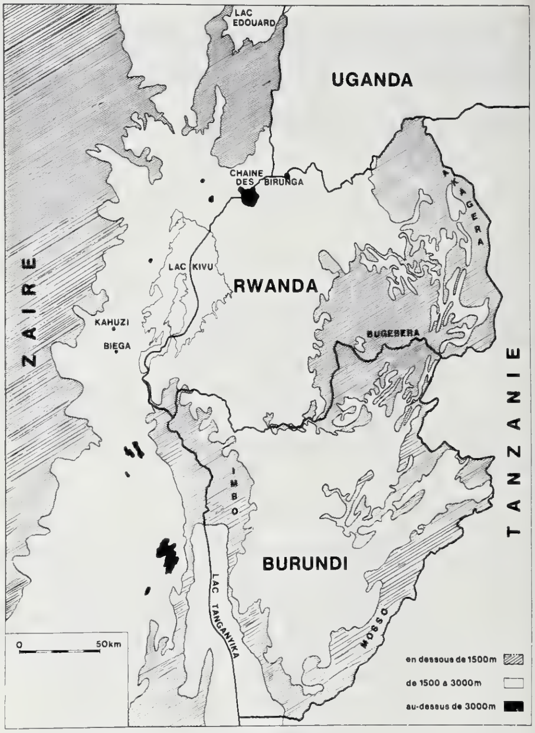

FIG. 1.—Carte de la zone prospectée au point de vue lichénologique par l'un de nous (J.L.) depuis 1971.

(b) *Elément tempéré-tropical*

Cet élément comprend en fait des variantes importantes, en particulier:

—un type holarctique tempéré-orotropical (ou éventuellement, dans la zone intertropicale, limité aux montagnes africaines). Ex.: *Pseudevernia furfuracea* (L.) Zopf, *Hypogymnia physodes* (L.) Nyl., *H. tubulosa* (Schaer.) Havaas, *Bryoria fuscescens* (Gyeln.) Brodo & D. Hawksw., *Platismatia glauca* (L.) Culb. & C. Culb., *Baeomyces rufus* (Huds.) Rebent., *Lobaria pulmonaria* (L.) Hoffm.;

—un type 'inverse', antarctique tempéré-orotropical, peu répandu et illustré notamment par *Placopsis parellina* (Nyl.) Lamb et *Parmelia swinscowii* Hale*;

—un type océanique-tempéré-tropical, qui présente lui-même des nuances, l'une correspondant à des taxons relativement ubiquistes en région intertropicale [comme *Catillaria bouteillei* (Desm.) Zahlbr., *Byssoloma leucoblepharum* (Nyl.) Vain., *Parmelia reticulata* Tayl., *Heterodermia leucomela* (L.) Poelt, *Pseudocyphellaria aurata* (Ach.) Vain. et *Normandina pulchella* (Borr.) Nyl.], l'autre à des taxons essentiellement limités là aux zones d'altitude [ex.: *Sphaerophorus melanocarpus* (Swartz) DC., *Usnea*

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* A titre provisoire, le genre *Parmelia* est maintenu ici dans son sens large, même si nous sommes convaincus qu'il est préférable d'y reconnaître plusieurs genres distincts.

articulata (L.) Hoffm., *Pseudocyphellaria crocata* (L.) Vain. et *Parmelia endochlora* Leight.];

—un type méditerranéen-tropical concerne les taxons qui, en région tempérée, sont essentiellement liés aux zones à climat (sub)méditerranéen (ex.: *Parmelia crozalsiana* B. de Lesd.).

(c) *Elément pantropical*

Cet élément déborde fréquemment la zone intertropicale s.str., surtout dans des régions humides, et il est alors parfois difficile à délimiter par rapport au type océanique-tempéré-tropical. De nombreux lichens foliicoles appartiennent à l'élément pantropical [ex.: *Mazosia melanophthalma* (Müll. Arg.) R. Sant., *M. phyllosema* (Nyl.) Zahlbr., *Porina epiphylla* (Fée) Fée, *Bacidia apiahica* (Müll. Arg.) Zahlbr., *Lasioloma arachnoideum* (Krempelh.) R. Sant.]; c'est le cas aussi de pas mal de macrolichens, notamment: *Ramalina celastri* (Spreng.) Krog & Swinscow, *Parmelia andina* Müll. Arg., *P. tinctorum* Nyl., *P. cristifera* Tayl., *P. formosana* Zahlbr., *P. texana* Tucker., *Coccocarpia palmicola* (Spreng.) Arvidss. & D. Gall., *C. erythroxyli* (Spreng.) Krog & Swinscow, *Dirinaria applanata* (Fée) Awasthi, *Heterodermia comosa* (Eschw.) Follm. & Redón. Quelques espèces sont oropantropicales, distribuées donc dans diverses montagnes des régions intertropicales (ex.: *Stereocaulon pomiferum* Duvigneaud).

(d) *Elément paléotropical*

Les lichens largement distribués dans toutes les régions tropicales de l'Ancien Monde ne semblent pas être légion (ex.: *Parmelia wallichiana* Tayl., *Porina semecarpi* Vain., *Trichothelium alboatrum* Vain.), mais il faut avouer que l'information reste lacunaire à ce propos. Un cas intéressant est celui de taxons limités à l'est de l'Afrique mais se retrouvant jusqu'en Asie orientale [ex.: *Lobaria retigera* (Bory) Trevis., *Parmelia aptata* Krempelh., *P. ecaperata* Müll. Arg.] une variante orophytique est illustrée par *Parmelia nilgherensis* Nyl. et *Stereocaulon foliolosum* Nyl. var. *botryophorum* (Müll. Arg.) Lamb, ce dernier connu seulement de l'Himalaya et de la chaîne des Birunga.

(e) *Elément afro-néotropical*

C'est le cas de taxons largement distribués en Afrique et Amérique tropicales, remontant éventuellement jusqu'au sud-est des USA [ex.: *Heterodermia casarettiana* (Massal.) Trevis., *Parmelia hypocraea* Vain., *P. sphaerospora* Nyl., *Opegrapha filicina* Mont., *Byssolecania deplanata* (Müll. Arg.) R. Sant.]. Une variante orophytique est à signaler, illustrée par *Stereocaulon atlanticum* (Lamb) Lamb et *Everniopsis trulla* (Ach.) Nyl. (connus seulement l'un et l'autre, en Afrique, des montagnes de l'est). Un cas plus intéressant est celui d'espèces limitées, dans le Nouveau Monde, aux contrées bordant la mer des Caraïbes et le golfe du Mexique, comme c'est le cas pour *Parmelia mordenii* Hale.

(f) *Elément guinéo-congolais (et congolais, le degré de prospection de cette flore lichénique rendant actuellement aléatoire la distinction)*

Les exemples typiques suffisamment connus actuellement seront empruntés aux épiphylles *(Porina kamerunensis* Schilling, *Opegrapha lambinonii* Sérusiaux, *Byssoloma vezdanum* Sérusiaux, . . .); d'autres exemples sont certainement à trouver dans les pyrénolichens, les Graphidales et les Thelotremataceae épiphytes.

(g) *Elément soudano-zambésien*

Ex.: *Parmelia rodriguesiana* Hue, *P. stuhlmannii* Dodge, *P. pseudocrinita* des Abb.

(h) *Elément zambésien-afrooriental et zambésien (la délimitation étant souvent encore prématurée)**

Ex.: *Parmelia amplexa* Stirt., *P. concrescens* Vain., *P. nairobiensis* Steiner & Zahlbr., *P. soyauxii* Müll. Arg., *Ramalina hoehneliana* Müll. Arg.

(i) *Elément de la région des lacs centrafricains (au sens de Denys, 1980)*

L'originalité de cette phytochorie récemment individualisée (White, 1979; Denys, 1980) se retrouve dans l'existence de quelques taxons semblant endémiques à cette région. Ex.: *Parmelia subtortula* Hale, *P. subcolorata* Hale.

(j) *Elément afromontagnard*

Distribué essentiellement dans l'étage des forêts de montagne de la région afromontagnarde telle que délimitée par exemple par Denys (1980). Certains taxons occupent la plupart des domaines de cette région, y compris le domaine ouest-africain (ex.: *Parmelia lobulascens* Steiner, *P. neodissecta* Hale, *Cladonia diplotypa* Nyl.), tandis que d'autres n'existent que dans les domaines orientaux et méridional (ex.: *Parmelia neutralis* Hale, *P. leiophylla* Kurok.) ou encore sont limités aux montagnes orientales ou centrorientales (ex.: *Parmelia pustulata* Hale, *Stereocaulon nigromaculatum* Duvigneaud, *S. furfuraceum* Duvigneaud, *Ramalina reducta* Krog & Swinscow, *R. disparata* Krog & Swinscow, *Cladonia hedbergii* Ahti, *Gyalideopsis lambinonii* Vězda).

(k) *Elément afroalpin*

Certains représentants de cet élément sont distribués dans l'étage alpin de plusieurs massifs (ex.: *Ramalina fimbriata* Krog & Swinscow), tandis que d'autres paraissent endémiques au domaine Kivu-Ruwenzori [ex.: *Stereocaulon humbertii* Duvigneaud, *Trapeliopsis haumanii* (Zahlbr.) G. Schneider, *Umbilicaria haumaniana* Frey, *Strangospora senecionis* Lambinon & Vězda].

4. CHOROLOGIE DES ESPÈCES DANS LA DITION ET ASPECTS DE LA VÉGÉTATION LICHÉNIQUE

Pour la zone prospectée par l'un de nous depuis 1971 (voir Lambinon & Sérusiaux, 1977; cf. aussi fig. 1), on dispose actuellement de quelques données autorisant plusieurs réflexions sur la chorologie des taxons dans cette dition et permettant une caractérisation des aspects les plus marquants du peuplement lichénique.

Les lichens largement répartis dans toute la dition sont peu nombreux, ce qui traduit évidemment

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* Certaines de ces espèces peuvent apparaître dans le houppier d'arbres de la forêt équatoriale, biotope à peine investigué jusqu'ici; elles devront le cas échéant être transférées dans une catégorie pluri-régionale africaine.

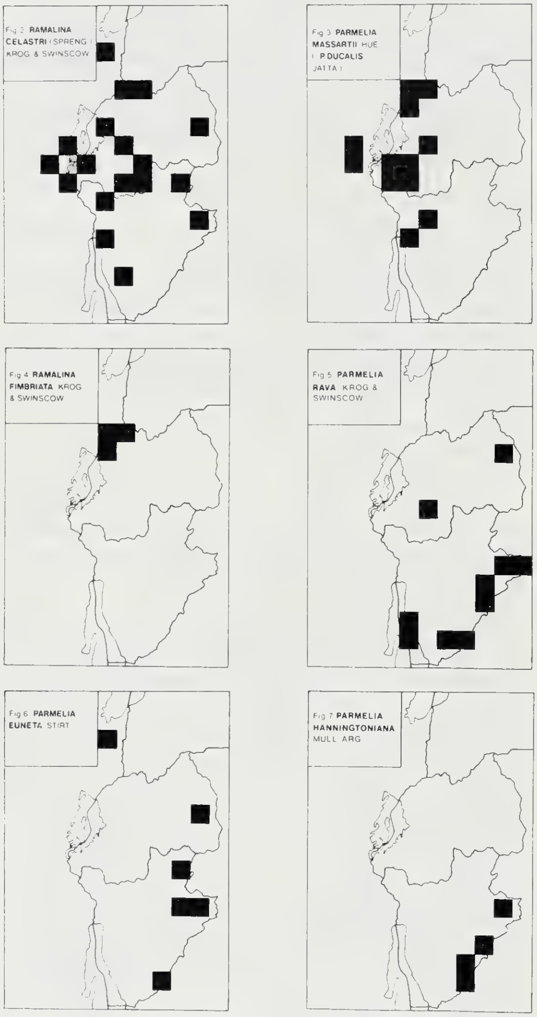
Fig 2 RAMALINA CELASTRI (SPRENG) KROG & SWINSCOW
Fig 3 PARMELIA MASSARTII HUE (= P. DUCALIS JATTA)
Fig 4 RAMALINA FIMBRIATA KROG & SWINSCOW
Fig 5 PARMELIA RAVA KROG & SWINSCOW
Fig 6 PARMELIA EUNETA STIRT
Fig 7 PARMELIA HANNINGTONIANA MULL ARG

FIGS 2–7.—Principaux types d'aires de distribution des lichens dans la dition.

la diversité biogéographique de celle-ci, liée à la variété du relief (l'altitude allant de 780 m au niveau du lac Tanganyika à 4 507 m au sommet du Karisimbi dans les Birunga), à celle des substrats et surtout des climats. On peut citer comme exemples quelques épiphytes banals dont certains peuvent d'ailleurs se retrouver localement à l'état rupicole ou subterricole; ainsi par exemple: *Parmelia andina* Müll. Arg., *P. reticulata* Tayl., *P. texana* Tucker., *P. nairobiensis* Steiner & Zahlbr., *Candelaria concolor* (Dicks.) Stein, *Dirinaria applanata* (Fée) Awasthi, *Ramalina celastri* (Spreng.) Krog & Swinscow (Fig. 2), *R. africana* (Stein) Dodge ou *Heterodermia leucomela* (L.) Poelt; à quelques exceptions près (notamment la dernière des espèces citées), ces lichens ne s'élèvent pourtant pas au-dessus de 2 500 m.

La petite portion du district forestier central incluse dans la dition n'a fait l'objet que de recherches fragmentaires. Dans la partie basse des troncs, le peuplement lichénique est essentiellement constitué d'espèces à thalle crustacé et à gonidies trentépohlioïdes (Pyrenulaceae, Trypetheliaceae Clathroporinaceae, Thelotremataceae, Gyalectaceae). Parmi les autres biotopes, n'a guère été étudié que le peuplement d'épiphylles; celui-ci est d'une richesse et d'une densité remarquables; il comprend souvent plus de 30 espèces sur un seul phorophyte et plus de 30% de la flore lichénique foliicole de la dition sont strictement limités à ce district. Un petit fragment de forêt qualifiée de périguinéenne (Lewalle, 1972), la forêt de Kigwena, existe au Burundi, en bordure du lac Tanganyika, mais son peuplement foliicole est beaucoup plus pauvre et sans affinités réelles avec la flore guinéo-congolaise du district forestier central.

La région afromontagnarde présente une flore lichénique souvent exubérante. Prise au sens large, elle comprend la forêt de montagne, un horizon à bambous (*Arundinaria alpina* K. Schum.), localement (dans la partie centrale des Birunga) des forêts-parcs à *Hagenia abyssinica* (Bruce) J.F. Gmel. et *Hypericum revolutum* Vahl, ensuite un étage de bruyères arborescentes (*Philippia johnstonii* Engl.), des paramos à *Dendrosenecio* et *Lobelia,* localisés aux Birunga et à la pointe sommitale du Kahuzi, et enfin, au Karisimbi, un étage pseudonival pratiquement dépourvu de végétation phanérogamique.

La flore des troncs de la forêt de montagne est surtout caractérisée par les *Parmelia* du groupe *'borreri'* (*P. subrudecta* Nyl., *P. rudecta* Ach. et *P. neutralis* Hale), du sous-genre *Hypotrachyna* [essentiellement *P. massartii* Hue (= *P. ducalis* Jatta) (Fig. 3), *P. formosana* Zahlbr., *P. orientalis* Hale et *P. endochlora* Leight.] et du sous-genre *Amphigymnia* (*P. crinita* Ach., *P. cooperi* Steiner & Zahlbr. et *P. subarnoldii* des Abb.); rares sont les espèces qui s'élèvent au-delà de la limite supérieure de la forêt de montagne, c'est-à-dire de 2 500 m. Les Caliciaceae sont représentées ici par un genre tropical, *Tilophoron,* avec deux espèces, *T. protrudens* Nyl. et *T. moderatum* Nyl. Les houppiers et les branches des arbres bordant les clairières et marais abritent en outre de nombreux lichens fruticuleux: des *Usnea,* des *Ramalina* (notamment *R. disparata* Krog & Swinscow), *Everniopsis trulla* (Ach.) Nyl, *Heterodermia leucomela* (L.) Poelt, . . . Dans les vallons humides de la partie inférieure de cet horizon, des Stictaceae [*Sticta weigelii* (Ach.) Vain., *S. fuliginosa* Ach., *Pseudocyphellaria crocata* (L.) Vain., *Lobaria retigera* (Bory) Trevis., . . .], des Collemataceae (e.a. des *Leptogium* sect. *Mallotium*), des *Coccocarpia* et *Pannaria* jouent un rôle prédominant. La flore foliicole est riche, caractérisée sourtout en-dessous de 2000 m par les *Porina* et les Asterothyriaceae, dont le nombre d'espèces diminue fortement plus haut, où les *Strigula* prennent une importance caractéristique. Les talus des roches pourries sont d'abord colonisés par *Baeomyces rufus* (Huds.) Rebent., *B. fungoides* (Swartz) Ach. et surtout trois *Stereocaulon* formant de remarquables peuplements: *S. furfuraceum* Duvigneaud, *S. nigromaculatum* Duvigneaud et *S. anomalum* Lamb; dans des stades plus évolués, se rencontrent entre autres *Cladonia diplotypa* Nyl. (qui est volontiers épiphyte dans le bas des troncs), *C. hedbergii* Ahti, des *Peltigera* et souvent de grands lichens foliacés plus habituellement épiphytes.

La flore bambusicole est caractérisée par un peuplement macrolichénique rappelant celui des branches de la forêt de montagne et par la présence de quelques espèces ordinairement foliicoles [ex.: *Byssoloma subdiscordans* (Nyl.) P. James].

L'étage à *Hagenia-Hypericum* et celui des bruyères arborescentes présentent un peuplement épiphytique bien individualisé. Certaines espèces de la forêt de montagne s'élèvent bien entendu jusqu'à ces altitudes (ex.: *Parmelia massartii* Hue), mais d'autres trouvent un optimum évident ou même se cantonnent à ce niveau (ex.: *Parmelia densirhizinata* Kurok., *P. lobulascens* Steiner, *Ramalina reducta* Krog & Swinscow). Les Caliciaceae sont ici de type boréal, avec notamment *Calicium trabinellum* Ach., *Coniocybe furfuracea* (L.) Ach., *Chaenotheca trichialis* (Ach.) Th. Fr. et *Ch. chrysocephala* (L.) Ach. Sur les branches, notamment de *Philippia*, les draperies d'*Usnea* sont particulièrement spectaculaires, mais l'étude du matériel reste à faire pour la dition.

Le peuplement des troncs de *Dendrosenecio* [ici *Senecio johnstonii* Oliv. subsp. *refractisquamatus* (De Wild.) Mabb.] compte certaines espèces en commun avec les épiphytes des *Hagenia* et des *Hypericum*, mais il s'individualise par des lichens tels que *Ramalina fimbriata* Krog & Swinscow (Fig. 4), *Lasallia papulosa* (Ach.) Llano var. *laceratula* (Vain.) Llano, *Coniocybe gracillima* Vain., des Stictaceae, des *Peltigera*, . . .

Les biotopes rocheux, en particulier les laves des Birunga, sont colonisés à partir d'environ 3 000 m par de nombreux *Stereocaulon: S. pomiferum* Duvigneaud, *S. ramulosum* (Swartz) Räusch., *S. meyeri* Stein, *S. atlanticum* (Lamb) Lamb, *S. nigromaculatum* Duvigneaud et *S. furfuraceum* Duvigneaud, qu'accompagnent notamment *Placopsis parellina* (Nyl.) Lamb et *Gyalidea dodgei* Vězda. Des parois rocheuses plus ou moins verticales portent entre autres *Usnea haumanii* Motyka, *U. bornmuelleri* Steiner, *Ramalina fimbriata* Krog & Swinscow, *Bryoria chalybeiformis* (L.) Brodo & D. Hawksw. (une seule récolte, au Muhabura) et, à des endroits humides, des plages filamenteuses noires formées par *Cystocoleus ebeneus* (Dillwyn) Thwaites ou *Racodium rupestre* Pers. Enfin, à plus de 4 000 m, dans l'étage surmontant les paramos, se rencontrent *Stereocaulon vesuvianum* Pers. var. *kilimandscharoense* Stein, *S. humbertii* Duvigneaud, *Umbilicaria haumaniana* Frey et *Omphalodiscus africanus* (Jatta) Llano.

Redescendons maintenant de ces sommets pour passer à des zones de plus basse altitude, à caractère tropical sensu stricto accusé, en évoquant d'abord brièvement la plaine de lave qui borde le nord-est du lac Kivu. Ici, entre 1 500 et 1 900 m, la colonisation des laves plus ou moins récentes se fait par d'immenses gazonnements de *Stereocaulon vesuvianum* Pers. var. *lebrunianum* Sérusiaux; sur les surfaces rocheuses plus lisses, ce sont surtout des *Parmelia* (notamment *P. concrescens* Vainio et *P. subramigera* Gyeln.) qui apparaissent en pionniers.

Les zones de moyenne altitude, qui se situent approximativement entre 1 600 et 1 900 m et correspondent principalement au 'district du Ruanda-Urundi central' de Lebrun (1956), sont généralement très anthropisées. Leur végétation lichénique épiphytique se limite donc essentiellement au peuplement d'arbres isolés ou en plantations *(Eucalyptus, Casuarina, Cupressus*, . . .). Celui-ci est fait de *Parmelia*, de Physciaceae (*Pyxine, Dirinaria, Physcia* s.l.,), de *Candelaria* [*C. concolor* (Dicks.) Stein et *C. fibrosa* (Fr.) Müll. Arg.], de *Ramalina*, de petits *Usnea* du groupe d'*U. complanata* (Müll. Arg.) Motyka, . . . Quelques rares espèces de la forêt de montagne s'y retrouvent sporadiquement [*Parmelia endochlora* Leight., *P. crinita* Ach., *Ramalina disparata* Krog & Swinscow, . . .], tandis que des lichens photophiles plus typiques des forêts sèches et des savanes y pénètrent volontiers [ex.: *Parmelia rava* Krog & Swinscow (Fig. 5), *P. hababiana* Gyeln., *P. isidiza* Nyl., . . .].

Les forêts sèches et savanes tropicales présentent généralement un épiphytisme bien développé et bien individualisé; fait exception l'Imbo (surtout sa partie nord), au Burundi, où les lichens sont rarement présents en dessous de 1 100 m. Parmi les espèces caractéristiques et largement répandues dans ces biotopes, on peut citer *Parmelia isidiza* Nyl., *P. ecaperata* Müll. Arg., *P. euneta* Stirt. (Fig. 6), *P. rava* Krog & Swinscow. Le peuplement des branches (notamment sur les bordures des bosquets xérophiles) est riche en *Ramalina* [*R. celastri* (Spreng.) Krog & Swinscow et *R. africana* (Stein) Dodge en particulier], *Heterodermia* [*H. leucomela* (L.) Poelt, *H. comosa* (Eschw.) Follm & Redón, . . .], *Teloschistes*, . . . Dans les bosquets xérophiles eux-mêmes, les Stictaceae et les Collemataceae sont souvent bien représentées. Une certaine flore foliicole s'y rencontre sporadiquement, encore qu'elle soit mieux développée dans les galeries forestières. Si sa richesse n'est guère comparable à celle des forêts de la dition, elle n'en rappelle pas moins certains faciès de la forêt de montagne, au point qu'on peut parler de satellites de cette flore foliicole montagnarde au sein de la région soudano-zambésienne. Dans cette zone, et d'ailleurs aussi plus haut dans la partie très cultivée ou pâturée du Rwanda et du Burundi, les affleurements rocheux portent divers lichens crustacés, dont le plus spectaculaire est certainement *Caloplaca cinnabarina* (Ach.) Zahlbr., qui forme des plages orange vif étendues; parmi les espèces foliacées saxicoles exclusives, on retiendra surtout *Parmelia pseudograyana* Hale, *P. grayana* Hue, *P. stuhlmannii* Dodge, *P. soyauxii* Müll. Arg. et plusieurs espèces du sous-genre *Xanthoparmelia* (*P. subramigera* Gyeln., *P. weberi* Hale et des espèces du groupe de *P. congensis* Stein).

Enfin, le district du Mosso-Malagarasi, petite portion à caractère zambésien de la partie sud et sud-est de la dition (cf. e.a. Reekmans, 1981), montre évidemment une flore lichénique du type de celle décrite pour l'ensemble des forêts sèches et savanes. Quelques espèces épiphytiques semblent pourtant l'individualiser localement: *Parmelia hanningtoniana* Müll. Arg. (Fig. 7), *P. amplexa* Stirt., *P. durumae* Krog & Swinscow et *P. pseudocrinita* des Abb., bien que les deux dernières soient en fait des taxons largement distribués dans la région soudano-zambésienne.

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Le recensement des plantes vasculaires et les originalités du peuplement végétal des monts Loma en Sierra Leone (Afrique Occidentale)

P. JAEGER*

RÉSUMÉ

Nos recherches sur la flore des monts Loma et les pays de piedmont (Sierra Leone) nous ont permis d'inventorier, en dernière analyse, un ensemble de 1 576 espèces, sous-espèces ou variétés d'Angiospermes; elles se groupent en 757 genres et 135 familles. Les Gymnospermes font défaut.

Comme pour toute autre région naturelle, la flore actuelle du Loma est l'aboutissement d'un processus long et complexe qui s'est déroulé au cours des époques révolues. Sous l'influence des facteurs climatiques, de migrations, de spéciation et aussi d'actions anthropiques, des unités floristiques d'origine très variée se sont finalement ordonnées en une mosaïque particulièrement diversifiée, mais instable dont il nous appartient de dévoiler les mécanismes qui ont présidé à leur mise en place.

ABSTRACT

A FLORISTIC INVENTORY OF THE LOMA MOUNTAINS IN SIERRA LEONE

Our surveys in Sierra Leone of the flora of the Loma Mountains and the foothill country have enabled us to produce an inventory of the 1 576 species, subspecies or varieties of Angiosperms belonging to 757 genera and 135 families. Gymnosperms are lacking.

As in any other natural region, the Loma flora is the result of a long and complex process which took place in much earlier times. Under the influence of climatic factors, migration, speciation and also anthropological action, floristic elements with very different origins have ultimately arranged themselves into a particularly diversified but unstable mosaïc and it is for us to unravel the mechanisms that have brought this about.

Comme l'a dit A. Chevalier en 1928, l'explication rationnelle du peuplement animal et végétal des montagnes ouest-africaines ne pourra être trouvée que le jour oú l'on connaîtra á fond la faune et la flore de l'ensemble de ces massifs.

En dépit de nos tournées totalisant un séjour de plus de 12 mois dans les monts Loma, en saison pluvieuse, en saison séche, ainsi que pendant les époques charnières, nous n'avons pas la prétention d'avoir fourni un inventaire complet des plantes vasculaires du massif. Il n'en reste pas moins que nos investigations et la mise sur pied d'un herbier de plus de 10 000 n^{os} permettent de se rendre compte, ne serait-ce que d'une façon approchée, de l'ampleur du peuplement végétal de ce massif sierra-léonais.

Le dernier dénombrement des récoltes effectuées dans le massif du Loma et des pays de piedmont, a révélé la présence de 1 576 espèces, sous-espèces ou variétés de végétaux vasculaires se répartissant en 757 genres et 135 familles (sont exclues les familles des Cryptogames), état de choses qui est résumé dans le tableau ci-contre.

Remarquons l'absence de Gymnospermes dont les stations les plus proches se situent à plus de 1 000 km à l'E du Loma: au Bénin (*Encephalartos barteri*) et au Cameroun (*Podocarpus milanjianus*).

Les Dialypétales-Apétales représentent le bloc de beaucoup le plus important quant au nombre des familles (87), des genres (341) et des espèces (671). De l'ensemble, l'ordre des Léguminosales émerge avec un total de 77 genres et 156 espèces; 15 genres et 25 espèces reviennent aux Mimosacées, 20 genres et 30 espèces aux Césalpiniacées, 42 genres et 101 espèces aux Papilionacées.

Les Gamopétales sont marquées par la supériorité écrasante des Rubiacées avec 110 espèces réparties en 49 genres; elles sont suivies de près par les Composées avec 70 espèces et 32 genres.

Chez les Monoctylédones le centre de gravité est occupé par les Graminées avec 117 espèces et 52 genres; de cette famille, la plus riche qui ait été recensée dans les monts Loma, est á rapprocher celle des Orchidacées (76 espèces et 31 genres) et celle des Cypéracées (64 espèces et 17 genres).

Mises à part 4 espèces de Lycopodes et 8 espèces de Sélaginelles, les Cryptogames vasculaires sont représentés essentiellement par 40 genres et 94 espèces de Ptéridophytes Filicales; parmi elles le genre *Asplenium* l'emporte sur tous les autres avec un ensemble de 18 espèces.

Comme pour toute autre région naturelle, la flore actuelle des monts Loma est l'aboutissement d'un processus long et complexe qui s'est déroulé au cours des époques révolues. Sous l'influence de facteurs climatiques, de migrations, de spéciations et aussi d'actions anthropiques, des unités floristiques d'origine très variée se sont finalement ordonnées en une mosaïque particuliérement diversifiée, mais instable, dont il nous appartient de dévoiler les mécanismes qui ont présidé à leur mise en place.

En raison de sa position à l'extrémité nord-ouest de la dorsale guinéenne, en raison aussi de sa proximité des contreforts méridionaux du Fouta Djalon, le Loma, sur le plan floristique et

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TABLEAU 1.—Analyse de la flore des monts Loma et des pays de piedmont

Taxons supérieurs	Familles Nombre	Familles %	Genres Nombre	Genres %	Espèces Nombre	Espèces %
Dialypétales-Apétales	87	64,4	341	45,04	671	42,5
Gamopétales	22	16,3	214	28,26	425	26,9
Monocotylédones	26	19,2	160	21,13	374	23,7
Cryptogames vasculaires	—	—	42	5,54	106	6,7
Totaux	135	99,9	757	99,97	1 576	99,8

phytogéographique présente d'étroites affinités avec l'un et l'autre de ces deux complexes montagneux; néanmoins, la présence de certaines espéces et groupements végétaux lui confère une originalité qui lui est propre et qui le distingue des autres massifs ouest-africains.

Près de la limite nord du Fouta Djalon, vers 1500m, dans des forêts où *Parinari excelsa* règne en maître, Schnell (1970) signale encore diverses espèces de la sylve méridionale hygrophile que l'on connait également du Loma; à savoir: *Uapaca chevalieri, Carapa procera, Garcinia smeathmannii, Memecylon fasciculare, Eugenia pobeguinii* . . ., ces résidus forestiers témoignent d'une extension ancienne vers le nord de la forêt guinéo-congolaise; au cours de son avancée, pendant des phases climatiques humides, cette vague forestière a dû submerger de vastes territoires ouest-africains actuellement couverts de savanes arborées.

En prairie d'altitude et sur les affleurements rocheux, les affinités entre le Fouta Djalon et le Loma sont soulignées par la présence d'orophytes endémiques comme: *Leocus pobeguinii, Nerophila gentianoides, Dissotis leonensis;* ce dernier, un arbrisseau à voûte hémisphérique au feuillage gris-cendré, est responsable de la formation, en altitude, de ce 'maquis' montagnard relictuel disloqué par les feux, dont les lambeaux se sont maintenus sur les sommets rocheux.

Sont également limitées au Loma et au Fouta Djalon, sans pour autant être rivées à l'altitude, des espèces comme: *Crassocephalum guineense, Dissotis pobeguinii, Eriocaulon irregulare, Erlangea fruticosa, Mesanthemum auratum, Sebaea luteo-alba, Utricularia micropetala* var. *macrocheilos*. Des orophytes prairiaux comme *Aristea angolensis* et *Hypoxis angustifolia* sont connus du Loma et du Fouta Djalon; mais leur aire, très vaste, s'étend jusqu'en Afrique orientale et australe pour le premiér jusqu'à Madagascar pour le second; ni l'un ni l'autre ne sont connus du Nimba; l'Hypoxidacée par contre existe au Fon (Schnell, 1961) *Impatiens jacquesii,* fréquent au Loma où il est inféodé aux rochers humides et ombragés, se retrouve dans des biotopes analogues au Fouta Djalon et au Benna; cette espèce n'est pas signalée au Nimba où à sa place, dans les stations humides, on trouve *Impatiens irvingii* (Schnell, 1961).

L'herbe rudérale, *Centella asiatica,* mise à part, le Loma n'abrite aucune des Ombellifères ligneuses ou herbacées du Fouta Djalon, comme *Steganotaenia araliacea, Pycnocycla ledermannii, Pimpinella praeventa;* et il en est de même des espèces xériques comme *Aloe barteri, Echinops longifolius, Dicoma sessiliflora,* qui se retrouvent dans des régions septentrionales plus sèches (massif de Kita, Plateau de Jos . . .).

Le Loma et toute la dorsale guinéenne sont exclus de l'aire que couvre *Microdracoides squamosus,* Cypéracée endémique de l'ouest africain, dont les Gbengbe Hills, à environ 40 km au nord de Makeni, consitituent, avec le Benna, la station la plus proche du Loma (Morton, 1966). Inversement, *Afrotrilepis pilosa,* une saxicole héliophile édificatrice de sols tourbeux, colonise les reliefs rocheux depuis le Fouta Djalon jusqu'au Cameroun et au Gabon; son aire englobe la totalité de la dorsale guinéenne (Raynal, 1963).

Plus étroites encore qu'avec le Fouta Djalon sont les affinités du Loma avec les massifs de la dorsale guinéenne, qu'ils soient situés au nord (Fon, Simandou) ou au sud (Ziama, Nimba, massif des Dans) de la limite actuelle de la forêt dense. Grâce aux travaux de R. Schnell et de J. G. Adam, le Nimba est aujourd'hui le mieux connu de tous les massifs méridionaux quant à sa flore et sa végétation.

En raison d'une différence latudinale sensible — Loma: 9°00′ à 9° 17′, Nimba: 7° 25′ à 7° 45′ L.N. — une pluviosité moindre est sans doute responsable de l'absence au Loma d'un certain nombre d'espéces typiquement ombrophiles connues du Nimba: *Lophira alata, Combretodendron africanum, Turraeanthus africanus, Xylopia staudtii, Enantia polycarpa.*

Cependant, au pied du versant ouest du Loma, dans la région la plus arrosée et la mieux abritée de l'harmattan, s'est conservé un lambeau de forêt dense ombrophile à *Heritiera utilis,* qu'on peut considérer comme l'homologue occidental de ce même type forestier que R. Schnell décrit au fond de la vallée du Ya, dans la fraction sud-ouest la plus humide du Nimba (Schnell, 1952).

La signification de cet îlot forestier ombrophile du Loma est manifestement relictuelle: le bloc forestier guinéo-occidental en se rétrécissant lors d'une phase climatique aride, a constitué dans les stations les mieux abritées ces 'bastions de refuge' propices à la survie d'espèces ombrophiles comme

Heritiera utilis, Cephaëlis biaurita, Mapania linderi, M. rhynchocarpa, Guaduella oblonga . . .

Quatre des dix familles endémiques de l'Afrique tropicale sont représentées en forêt dense ou dans les lisières forestières du Loma. Ce sont toutes des familles peu riches en genres et en espèces, ce qui est 'indicative of the low level of speciation already noted in the guineo-Congo Region' (Brenan, 1978).

Citons:
les *Dioncophyllacées* avec *Triphyophyllum peltatum;*
les *Octoknématacées* avec *Octoknema borealis;*
les *Mélianthacées* avec *Bersama abyssinica* subsp. *paullinioïdes;*
les *Napoléonacées* (partie des Lécythidacées) avec *Napoleona leonensis, N. vogelii.*

Au Nimba, on remarque en plus la famille des *Médusandracées,* qui y est représentée par *Soyauxia floribunda,* petit arbre non encore cité du Loma.

En étudiant les forêts montagnardes des Dans et du Nimba, Aubréville (1932) et Schnell (1952) ont été frappés par la faible contribution que prend l'élément orophile dans l'édification de cette sylve où certaines espèces de basse altitude atteignent une importance inattendue. Et il en est de même au Loma où divers taxons apparemment rivés à l'altitude comme: *Syzygium staudtii, Afrosersalisia cerasifera, Ficus eriobotryoïdes, Uapaca chevalieri, Coffea ebracteolata, Ochna membranacea, Eugenia leonensis, Schefflera barteri, Solenostemon repens . . .* sont cependant issus de la flore planitiaire ou lui sont étroitement apparentées; le cas le plus frappant étant celui du *Parinari excelsa.*

La forêt montagnarde du Loma se distingue de celle des autres massifs de la dorsale, du Nimba en particulier, par la présence autour de 1 000 m de peuplements, parfois importants, d'*Oxytenanthera abyssinica.* Commun à basse altitude dans les savanes soudaniennes (Kita) et soudano-guinéennes, ce Bambou déjà signalé au Loma par Bakshi (Keay & Hepper, 1958–1972) y occupe une station manifestement décalée par rapport à la limite méridionale de son aire.

Les espèces endémiques appartenant en propre au Loma sont actuellement au nombre de neuf; cette valeur, très faible, risque de varier par la suite dans un sens ou dans l'autre, au hasard des prospections. En ce jour nous relevons:

Afrotrilepis jaegeri
Digitaria phaeotricha var. *patens*
Dissotis sessilis
Gladiolus leonensis
Ledermanniella jaegeri
Loudetia jaegeriana
Loxodera strigosa
Schizachyrium minutum (= *S. brevifolium*)
Scleria monticola.

Ce sont toutes des orophytes localisés en prairie montagnarde ou dans les biotopes rocheux; et il en est de même de celles du Nimba, à cette différence près, que ces deux lots sont entiérement étrangers l'un à l'autre sur le plan taxonomique, particularité qui permet non seulement de souligner l'originalité floristique de chacun de ces deux sommets ouest-africains, mais aussi de saisir l'influence manifeste de cette 'oro-insularité' sur la diversification spécifique. A ce sujet, rappelons que — *l'Osbeckia porteresi* et *Blairia nimbana* n'ont jamais été observés au Loma, pas plus que *Nectophrynoides occidentalis,* crapaud vivipare découvert en 1942 au Nimba par M. Lamotte. Inversement, il convient de faire remarquer que jusqu'à ce jour, *Afrotrilepis jaegeri* n'a jamais été signalé en dehors du complexe montagneux Loma-Tingi.

Non moins intéressantes que les endémiques propres au Loma sont ceux des orophytes qui, sans affinités avec les espèces planitiaires, se retrouvent sur d'autres sommets ouest-africains et même dans divers massifs est-africains distants du Loma de plusieurs milliers de kilomètres; entre autres, citons: *Cynanchum praecox, Drosera pilosa, Euphorbia depauperata, Habenaria jaegeri, Homalocheilos ramosissimus, Helichrysum mechovianum, Thesium tenuissimum . . .*

La présence de ces mêmes espèces (parfois il s'agit de taxons infra-spécifiques) en des points géographiquement aussi éloignés ne semble pouvoir s'expliquer, à première vue, que par le transport à longue distance de diaspores ou par la fragmentation d'aires anciennement continues en îlots relictuels favorables à la conservation de ces plantes.

Divers auteurs se sont proposés de trouver une explication à ce problème, entre autres: A. Aubréville, A. Chevalier, A. S. Boughey, J. P. M. Brenan, Th. C. E. Fries, F. N. Hepper, J. Lebrun, L. Liben, J. K. Morton, H. N. Ridley, Du Rietz, R. Schnell, J. van Steenis, E. J. Weyland, H. Weimark, F. White . . .

L'étude de la dispersion à longue distance par le vent ou les oiseaux n'ayant abouti, dans la plupart des cas, qu'à une impasse, les auteurs se sont demandés si les vicissitudes climatiques des époques révolues ne pouvaient, dans une certaine mesure donner la clef du problème.

Les chutes thermiques du Quaternaire, loin de rester confinées aux seules régions septentrionales, se sont répercutées sur la presque totalité du globe. Aux glaciations boréales ont correspondu, sous les tropiques, des périodes pluviales marquées par un abaissement de la température et par une augmentation des précipitations; il en résulta un abaissement des étages de végétation et, partant, un accroisement de leur aire, suivi d'un rétrécissement des discontinuités, état de choses éminemment favorable aux migrations. Selon J. K. Morton, une chute thermique de 4° à 6° aurait provoqué un abaissement d'environ 1 000 m des étages de végétation. Ainsi, des reliefs modestes, véritables relais entre les massifs Est et Ouest africains, vont jalonner la 'route' et donner asile aux orophytes; car 'de très hautes altitudes ne sont pas nécessaires dans les régions tropicales pour qu'il existe une flore montagnarde' (Chevalier, 1929). Sur des reliefs modestes épars en Nigéria (Idanre et Ado Hills), au Ghana (Shai, Atewa, Banda Hills, Gambaga Scarp), en Sierra Leone (Gbenghe, Kuru Hills), susceptibles d'avoir fonctionné comme 'stepping stones' entre l'est et l'ouest, J. K. Morton signale 'a small and presumably relict montane flora.'

Tout porte à croire que le Loma, situé actuellement en pays de savane, était inclus jadis, au même titre que le Nimba, dans le domaine de la forêt dense humide guinéo-équatoriale.

Rappelons, en effet, la présence, au pied du versant ouest, de lambeaux forestiers ombrophiles à *Heritiera* et *Mapania,* et la présence sur les basses pentes du versant de vastes forêts denses humides décidues. Cette appartenance du Loma au bloc forestier guinéo-congolais est encore soulignée par l'absence de représantants de la famille des Ombelliféres; car, selon J. Félix 'il y a incompatibilité de fait entre les formations forestiéres équatoriales et le développement des Ombellifères' (Jaques-Félix, 1970). Ce caractère négatif, confirme l'originalité de la région guinéo-congolaise et, partant, celle des massifs de la dorsale, y compris le Loma.

En raison de sa situation marginale et aussi de sa latitude, le Loma, lors des avancées et des reculs du front forestier, a dû se trouver tantôt en deçà, tantôt, comme aujourd'hui, au-delà de cette limite de la forêt dense. La position actuelle s'est avérée éminemment favorable à l'intrusion massive, sur le versant est, d'espèces savanicoles. Sous l'influence des feux attisés par le souffle de l'harmattan 'les graminées ont pris une influence considérable au détriment de l'ancienne parure boisée' '(Aubréville, 1962).

Le Loma isolé en pays de savane au-delà des limites du bloc forestier guinéo-occidental est aussi exposé à une savanisation dont la rapidité et l'ampleur sont commandées, en grande partie, par les actions anthropiques.

Comme la vague ignée et le flot des Graminées qui lui succède, risque fort de mettre en péril la végétation endémique et relictuelle, soit une des orginalitée du Loma, il y a lieu de penser, sans trop tarder, à une protection efficace de ce massif ouest-africain.

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The phytogeography of Mount Kulal, Kenya, with special reference to Compositae, Leguminosae and Gramineae

F. N. HEPPER*

ABSTRACT

Mt Kulal, in the lowlying desert of NE Kenya, reaches an altitude of 2 295 m. A synopsis of the vegetation types occurring there is provided, with totals of the species recorded in each type. The three families are analysed phytogeographically and observations are made about their chorology. A conclusion is reached that Mt Kulal is a stepping stone for the distribution of montane plants between highland East Africa and Ethiopia and not an outlier of either bloc.

RÉSUMÉ

LA PHYTOGÉOGRAPHIE DU MONT KULAL, AU KENYA, EN SE RÉFÉRANT SPECIALEMENT AUX COMPOSEES AUX LÉGUMINEUSES ET AUX GRAMINÉES

Le Mont Kulal, dans le désert de basse altitude du nord-est du Kenya, atteint une altitude de 2 295 m. Un synopsis des types de végétation qui s'y rencontrent est établi, avec les inventaires complets des espèces relevées dans chaque type. Les trois familles sont analysées du point de vue phytogéographique et des observations sont faites sur leur chorologie. On arrive à la conclusion que le Mont Kulal est un relais dans la distribution des plantes montagnardes entre les hauts plateaux de l'africain et de l'Ethiopie et non un massif détaché de l'un ou l'autre bloc.

INTRODUCTION

The flora of the ancient basaltic outcrop known as Mount Kulal (c. 2°43'N, 36°55'E) in the Marsabit District of NE Kenya (Figs 1, 2 & 3) has been investigated in recent years to a degree considered sufficient for a preliminary phytogeographical analysis to be made. The basis for this study is a recently prepared annotated checklist (Hepper *et al.,* 1981). This list contains over 700 species of flowering plants and ferns. It is probably reasonably complete for the evergreen upland forest on its summit (Synnott, 1979), but the vast lower slopes are still imperfectly known; partly because of the ruggedness of the terrain which has hindered investigation of the vegetation, and partly owing to the rainfall being extremely erratic, causing the development of a highly adapted flora, with many species appearing or in a condition worth collecting for only a short time after rain when a collector may not be present.

However, a vegetation survey has been completed and a map of the mountain and surroundings in Marsabit District has been published (Herlocker, 1979) (Fig. 4). Therefore it is now possible to assign the plant species recorded on Mt Kulal to various vegetation types recognized by Herlocker (1979) as occurring there (Table 1). In spite of the comment made above about the lower slopes being imperfectly known, further collecting is unlikely to change the numerical superiority of the summit zones (Types 1–6 in Table 1), because they are very much moister than the middle and lower zones.

THE PHYTOGEOGRAPHICAL DIVISIONS OF AFRICA

Plant geographers now generally recognize the African divisions (regional phytochoria) published by White (1970), with the later boundary and nomenclatural modifications of Clayton & Hepper (1974), Wickens (1976) and Brenan (1978). These are shown in Fig. 5, whereas Table 2 provides a summary of the analysis of Compositae, Leguminosae and Gramineae. The groupings of the divisions have been made in order to combine those of lesser significance, while at the same time indicating aspects that are considered to be more important for this study. Thus the Afroriental Domain total is shown separate from the Sudano-Zambezian Region of which it is part. Endemics, however, are not

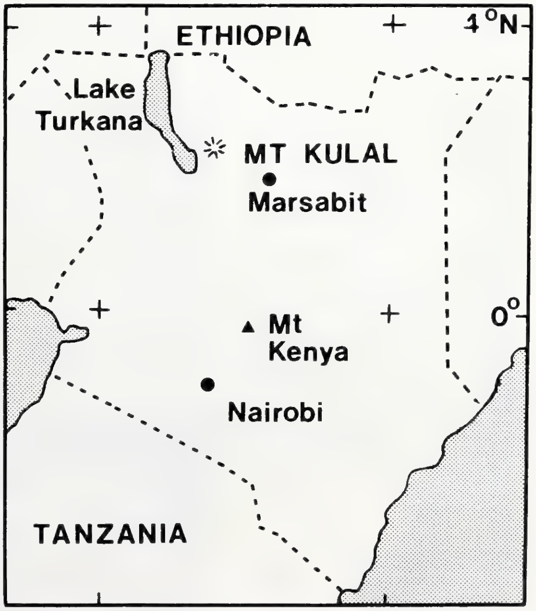

FIG. 1.—The location of Mt Kulal in East Africa.

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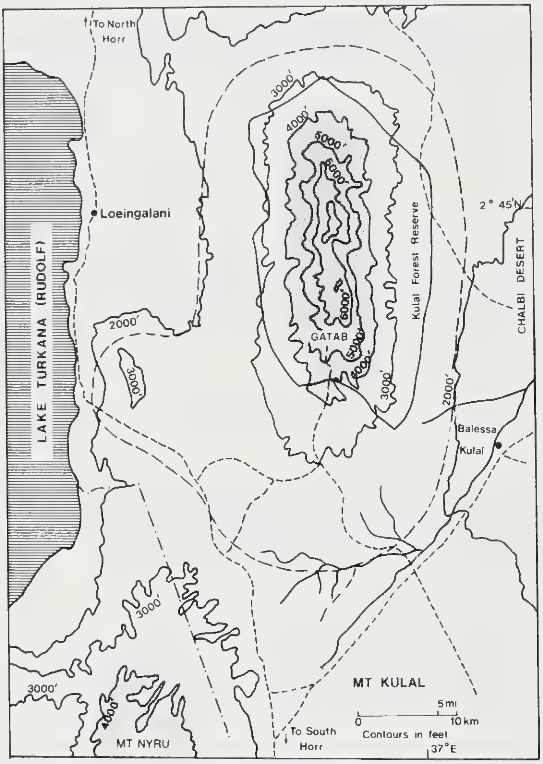

FIG. 2.—Contour map of Mt Kulal.

entered on the table, but they are mentioned in the following discussion. As might be expected from an isolated mountain situated in the driest desert area of eastern Africa, not one species is recorded for the Guineo-Congo element.

This analysis involves a total of 182 taxa i.e. species, subspecies and varieties, which is about 25% of the known Mt Kulal flora. There are 48 taxa belonging to the Compositae, 56 Leguminosae (in three subfamilies) and 78 Gramineae; these families have been selected for their large size and up-to-date taxonomy. However, in the discussion that follows examples are taken from other families when appropriate, because those three families have few woody species and they are poorly represented in the summit forest.

Saharo-Sindian Region

These are essentially desert or semi-desert plants having West-East distributions into the Sahara, e.g. *Oropetium minimum* extends from Chad to Somalia; *Tephrosia nubica* (Fig. 6) occurs from Niger to the Red Sea. Some reach as far east as India, e.g. *Eragrostiella bifaria, Eragrostis papposa, Indigofera coerulea* var. *occidentalis. Acacia senegal* (Fig. 7) has a wide distribution across Africa with a concentration in the Afroriental Domain.

Sudano-Zambezian Region

This encompasses the great arc of savanna around the humid Guineo-Congo Region from West Africa to East Africa, Angola and South Africa. However, this analysis shows there are surprisingly few species common to both the bulge of West Africa and to Mt Kulal, most of those entered for this region have a short westward extension. For example: *Helichrysum glumaceum* extends from Senegal to Tanzania in rather dry country of the Sahelian Domain, whereas *H. rhodolepis, Conyza pyrrhopappa* (Fig. 8) and *Crassocephalum mannii* occur at higher

FIG. 3.—Base of Mt Kulal, dry bed of Balessa River in foreground, basaltic slopes to right, summit hidden by clouds. Photo: F. N. Hepper.

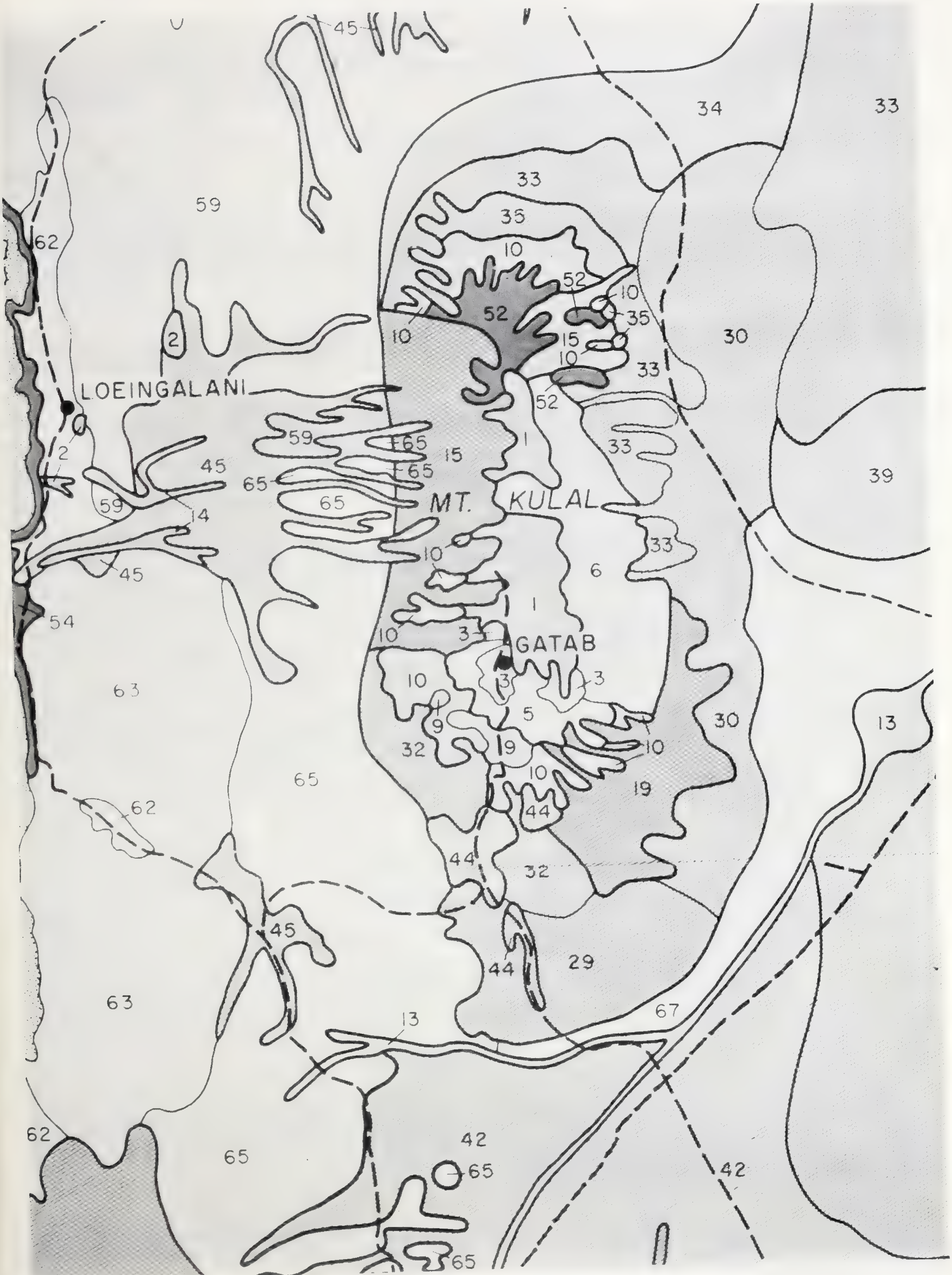

FIG. 4.—Portion of the vegetation map of S.W. Marsabit District relating to Mt Kulal (after Herlocker, 1979). Original in colour; see Table I for explanation of vegetation types.

TABLE 1.—Vegetation types recognised on Mt Kulal

	Vegetation type (after Herlocker, 1979)	Compositae, Leguminosae and Gramineae; no. of taxa recorded i.e. species, subspecies and varieties
Type 1	Upland Evergreen Forest: *Cassipourea, Diospyros, Olea, Teclea*	192
	(Dense forest)	(143)
	(Open glades and grassland)	(49)
Types 3–6	Evergreen to semi-deciduous Bushland	
	3. Evergreen Bushland: *Carissa, Euclea, Rhus, Juniperus*	249
	5. Semi-deciduous Bushland: *Euclea, Lippia, Ormocarpum*	138
	6. Composite Unit (numerous deep, steep walled canyons): Continuum of deciduous bushland through evergreen forest	47
Types 7–14	Woodland	
	Deciduous with dwarf shrub understorey:	
	9. *Acacia drepanolobium* with *Duosperma*	94
	10. *Acacia etbaica, A. nilotica* with *Duosperma*	59
Types 15–19	Bushland	
	15. Composite units: continuum of deciduous bushland through evergreen to semi-deciduous bushland	47
	19. Deciduous with succulent dwarf shrub understorey: *Acacia mellifera, A. reficiens, Commiphora* with *Euphorbia, Plectranthus*	11
Types 20–33	Shrubland	
	Deciduous with dwarf shrub understorey:	
	29. *Acacia mellifera, A. reficiens, Commiphora* with *Duosperma*	24
	30. *Acacia mellifera, A. reficiens* with *Duosperma, Sericocomopsis*	13
	Deciduous shrubland with succulent dwarf shrub understorey:	
	32. *Acacia mellifera, Commiphora* with *Euphorbia, Plectranthus*	18
Types 33–44	Dwarf shrubland:	53
	34. *Duosperma*	
	35. *Duosperma, Plectranthus*	
	36. *Duosperma, Indigofera*	
	44. Wooded dwarf shrubland, *Duosperma* with *Acacia tortilis*	
Types 46–54	Perennial Grassland:	
	52. Wooded upland grassland: *Bothriochloa, Themeda* with *Juniperus*	11
Types 55–72	Annual grassland:	50
	59. Dwarf shrub short: *Aristida* with *Duosperma, Indigofera Sericocomopsis*	
	63. Bushed dwarf short: *Cenchrus* with *Commiphora, Indigofera, Sericocomopsis*	
	65. Bushed dwarf short: *Aristida* with *Acacia mellifera, Commiphora, Jatropha, Indigofera*	
	67. Bushed dwarf short: *Aristida* with *A. mellifera, A. reficiens, Duosperma, Sericocomopsis*	

altitudes from Cameroun to Malawi and/or Angola; *Rhynchosia minima* var. *prostrata* occurs from Ghana round to South Africa; *Andropogon schirensis* goes the whole way from Senegal to South Africa.

Sudano-Zambezian Region, with extensions to Madagascar, Mediterranean or Deccan Regions

The species in this category have an even wider distribution than those in the last one. Species extending to Madagascar include *Spilanthes mauritiana, Indigofera arrecta* and *Sporobolus pyramidalis. Chloris pycnothrix, Hyparrhenia hirta* and *Reichardia tingitana* (Fig. 9) extend to the Mediterranean Region, and *Delonix elata, Bothriochloa insculpta* and *Digitaria abyssinica* extend to the Deccan Region.

Afroriental and Zambezian Domains, with extensions to the South Arabian Domain and/or the Madagascan Region

As a sub-division of the Sudano-Zambezian Region this gathers together the species with a wider Eastern African distribution than the following subdivision. They have distributions extending from southern to north-eastern Africa, e.g. *Aspilia mossambicensis, Indigofera schimperi* and *Lintonia*

TABLE 2.—Analysis of taxa in African phytogeographical divisions

Chorological Zone	Compositae 48 taxa no.	%	Leguminosae 56 taxa no.	%	Gramineae 78 taxa no.	%	Sum of taxa	% of 182
Saharo-Sindian Region	0	0	5	8,9	11	14,1	16	8,8
Sudano-Zambezian Region	6	12,5	6	10,7	11	14,1	23	12,6
Sudano-Zambezian Region, with extensions to Madagascar, Mediterranean and/or Deccan Regions	3	6,2	4	7,1	14	17,9	21	11,5
Afroriental and Zambezian Domains, with extensions to Madagascar and/or South Arabian Region	7	14,6	13	23,2	10	12,8	30	16,5
Afroriental Domain	17	35,4	23	41,0	14	17,9	54	29,6
Afromontane Domain	9	18,7	1	1,7	1	1	11	6,0
Pantropical, Palaeotropical	6	12,5	4	7,1	18	23,0	28	15,4

nutans. Others extend beyond Africa, for example, *Senecio petitianus* and *Mucuna gigantea* subsp. *quadrialata* cross to Madagascar, whereas *Psiadia punctulata, Pterolobium stellatum* and *Cypholepis yemenica* reach southern Arabia.

Afroriental Domain

This accounts for those species occurring in the north-east and east of Africa (Ethiopia, Somalia, Kenya, Tanzania). The figures in Table 2 for each of the three families reveal that a high percentage of the Mt Kulal species come into this category. An attempt to divide them into those with distribution southwards and those whose distribution is northwards proved difficult on a numerical basis. This is because, although a species may be concentrated in Ethiopia, and therefore be regarded as a north-eastern species, there are often outlying records

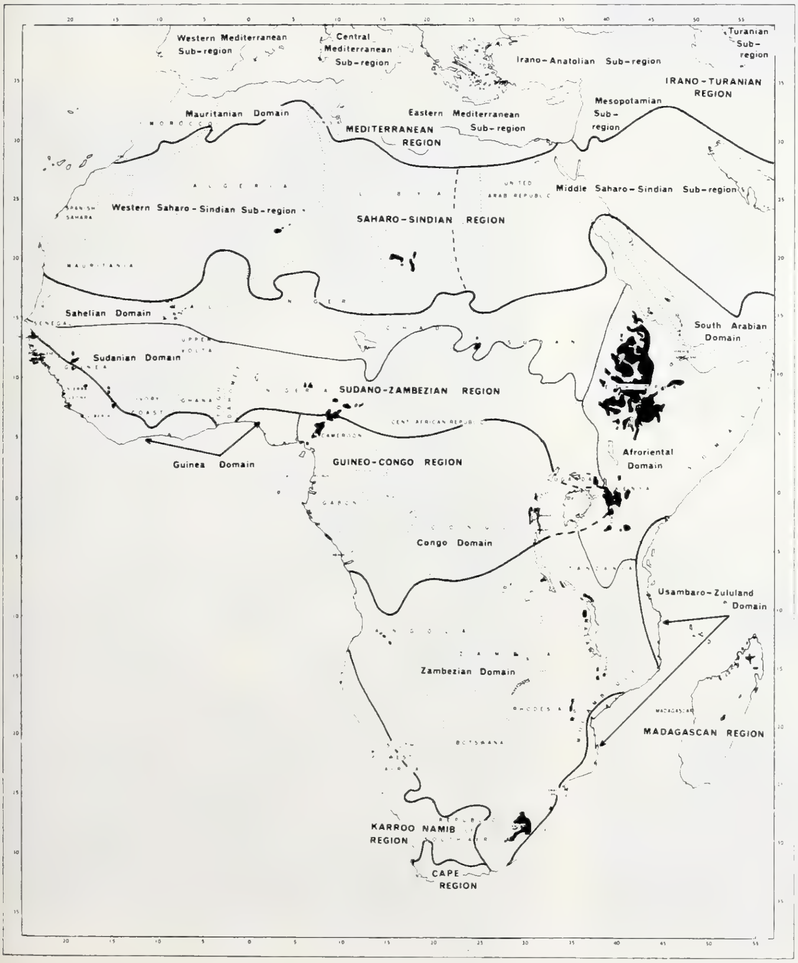

FIG. 5.—The phytogeographical divisions of Africa; the montane region in black (from Brenan, 1978).

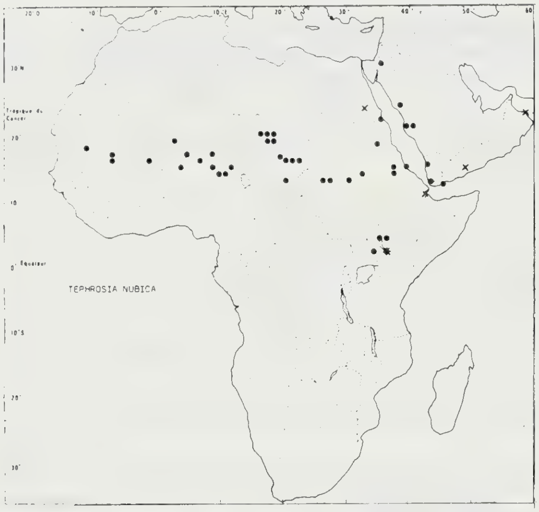

FIG. 6.—Distribution of *Tephrosia nubica*—Saharo-Sindian Region (from Lebrun, 1977).

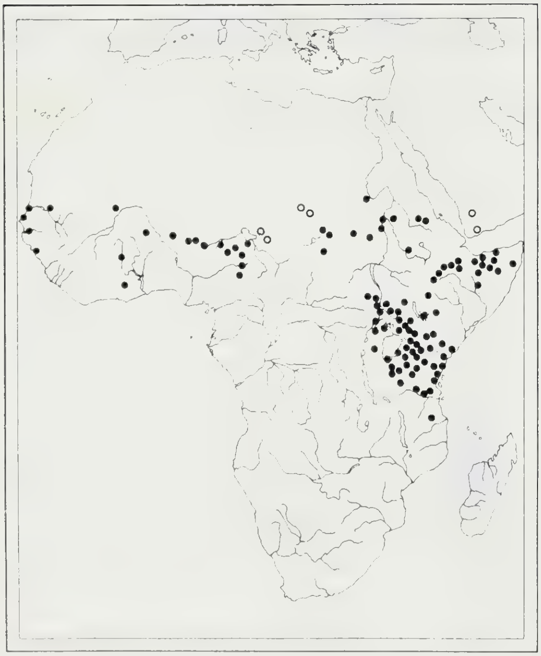

FIG. 7.—Distribution of *Acacia senegal* — Saharo-Sindian Region and Afroriental Domain (Wickens, 1976).

further south and vice versa which make it difficult to place on a presence or absence basis.

There is undoubtedly a very strong north-eastern element, including those occurring in the South Arabian Domain which is really a tropical extension into the Arabian Peninsula, e.g. *Senecio lyratipartitus, Cadia purpurea, Crotalaria emarginella, Tephrosia semipilosum, Eragrostis braunii, Pennisetum stramineum.* Some of the species are highland, e.g. *Cadia purpurea,* whereas others occur in the dry low country, e.g. *Tephrosia polyphylla, Drake-Brockmania somalensis.*

Turning to those with a southwards distribution there are some legumes limited to East Africa proper, e.g. *Crotalaria balbi, Erythrina burttii, Vigna friesiorum.* Compositae and Gramineae, however, seem to have a wider distribution. Many of the species that would come into this category in fact extend even further southwards into the Zambezian Domain already dealt with.

Afromontane Domain

This is a particularly interesting category but, since it is not well represented by the three families analysed, we shall take examples from other families.

The Afromontane Domain is discontinuous, being present wherever the summits are high enough, hence White (1981) regards it as an archipelago. Mt Kulal supports a number of such species and their presence in isolation poses problems of dissemination which are discussed on p. 550. The summit forest is composed mainly of *Olea hochstetteri* (Figs 10 & 11) with *Teclea nobilis, T. simplicifolius, Cassipourea congoensis* and a herbaceous ground layer of many Acanthaceae. A notable absentee is the genus *Podocarpus* *, which is present on the Ndotos and on Nyiru, some 80 km southwards. Whereas many of the species inhabit the montane forest, others occur in the open glades or grassland at higher altitudes. How such montane species reached Mt Kulal is discussed with other distributional problems on p. 550.

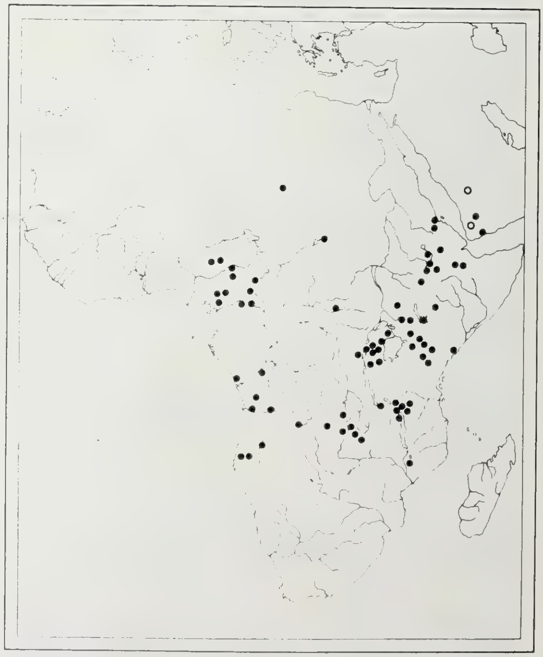

FIG. 8.—Distribution of *Conyza pyrrhopappa* — Sudano-Zambezian Region (from Wickens, 1976).

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* The sight record by Synnott (1979) is doubted by himself!

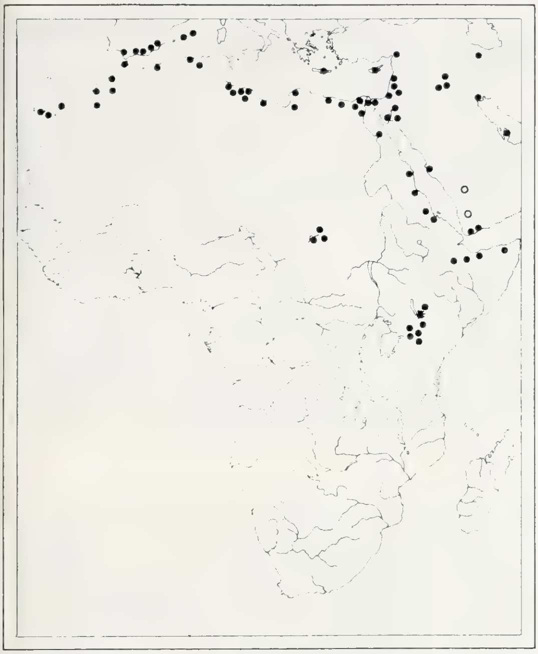

FIG. 9.—Distribution of *Reichardia tingitana* — Mediterranean and Saharo-Sindian Regions and the Afroriental Domain of the Sudano-Zambezian Region (from Wickens, 1976).

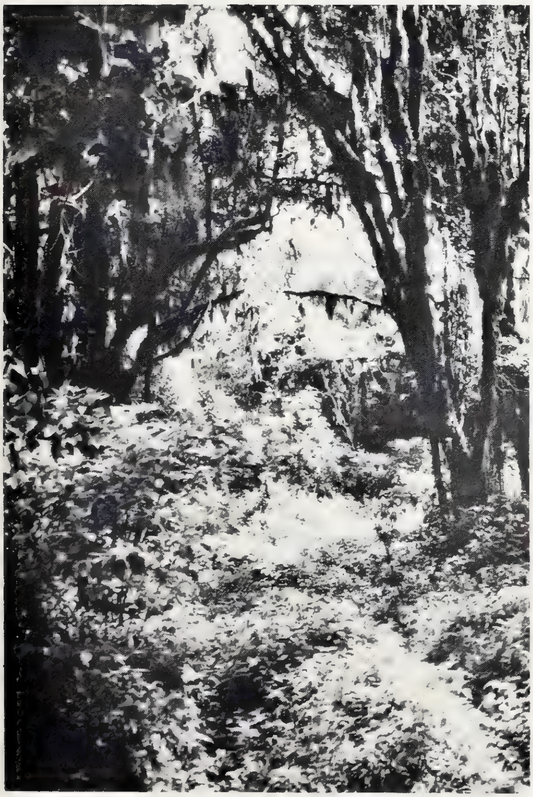

FIG. 10.—*Olea hochstetteri* forest with *Usnea* near summit of Mt Kulal. Photo: F. N. Hepper.

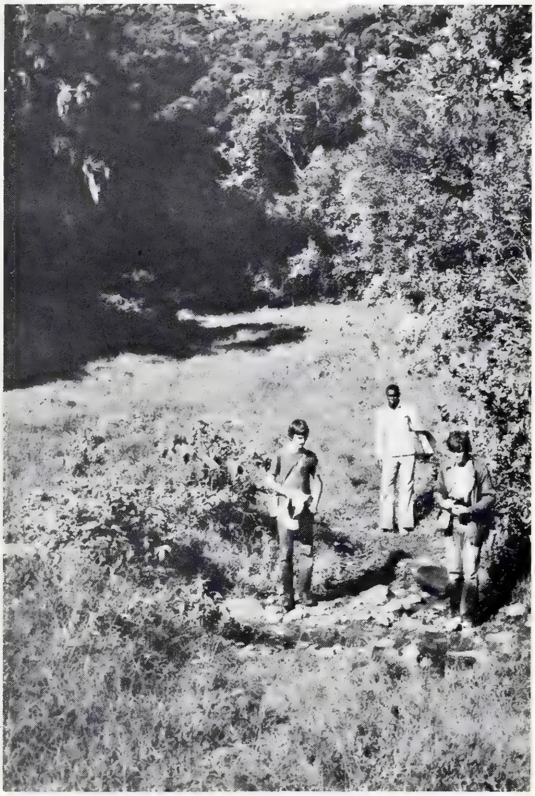

FIG. 11.—Glade with stream in montane forest below summit of Mt Kulal. Photo: F. N. Hepper.

Examples: *Cussonia holstii* (Araliaceae), *Silene burchelli* (Caryophyllaceae), *Cineraria grandiflora* (Compositae), *Crepis rueppellii* (Compositae) (Fig. 12), *Casearia battiscombei* (Flacourtiaceae), *Geranium arabicum* (Geraniaceae), *Xymalos monospora* (Monimiaceae), *Rapanea melanophloeos* (Myrsinaceae), *Rhamnus prinoides* (Rhamnaceae), *Psychotria orophila* (Rubiaceae), *Andropogon distachyos* (Gramineae) (Fig. 13).

Palaeotropical, pantropical, cosmopolitan

Some of the species are weeds unintentionally distributed by man. Mt Kulal has been settled for a relatively short time, although no doubt there have always been temporary dwellings and incursions by pastoralists, especially during prolonged droughts. With increasing contacts with the outside world through the Africa Inland Church and the United Nations project, an increase in the number of weedy species can be expected. Examples of weeds already occurring there are: *Stellaria media* (Caryophyllaceae), *Chenopodium murale* (Chenopodiaceae), *Ocimum suave* (Labiatae), *Malva parviflora* (Malvaceae), *Anagallis arvensis* (Primulaceae), *Physalis peruviana* (Solanaceae) and *Cynodon dactylon* (Gramineae). Two other grasses, *Eragrostis minor* and *Polypogon monspeliensis* are more temperate in requirements and have a Boreo-Atlantic distribution.

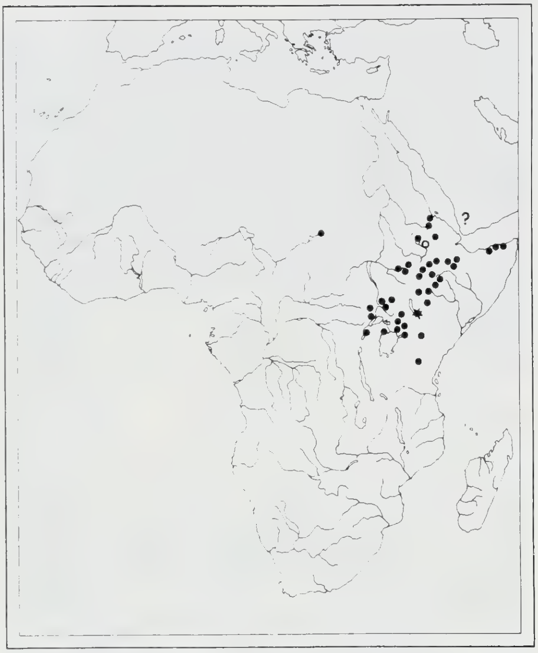

FIG. 12.—Distribution of *Crepis rueppellii* – Afromontane Domain, restricted to East Africa (from Wickens, 1976).

Other species having such wide distributions are not necessarily connected with man. They have occupied available habitats over a wide area and are of little interest from a phytogeographical point of view. Some are aquatics which have probably been distributed by water-birds, e.g. *Veronica anagallis-aquatica*. Others have fruits or seeds adapted for animal, especially bird, distribution, e.g. *Achyranthes aspera, Pupalia lappacea* (Amaranthaceae) and *Bidens pilosa* (Compositae). *Desmodium repandum* (Leguminosae) has a wide range in the palaeotropics as a plant of upland forest. Although most are herbaceous, some are woody, e.g. *Carissa edulis* (Apocynaceae), *Securinega virosa* (Euphorbiaceae) and *Scutia myrtina* (Rhamnaceae). It is significant that these bushes all have berries that are likely to be distributed by birds.

ENDEMICS ON MT KULAL

Insufficient is known about the number of endemics to be able to analyse them. However, there appear to be several endemics occurring at lower altitudes on the mountain, some of them are awaiting publication or assessment as to their taxonomic status. Several in the three families have been added to the Afroriental total. A tentative list of suspected endemics so far recorded is as follows: *Barleria* sp. (*Herlocker* 363), *Justicia* sp. (*Hepper & Jaeger* 6909), *Cadaba* sp. (*Bally* 5658), *Plectranthus* sp. (*Hepper & Jaeger* 7032), *Bidens* sp. (*Herlocker* 661, *Hepper & Jaeger* 6945), *Vernonia galamensis* (Cass.) Less. var. nov. (*Hepper & Jaeger* 6983), *Aloe* sp. 1 (*Bally* 5578, *Hepper & Jaeger* 7151), *Aloe* sp. 2 (*Bally* 5633, *Hepper & Jaeger* 7152) and *Polystachya* sp. nov. (Hepper & Jaeger 7086).

One would expect such an ancient base-rich volcanic mountain to possess more endemics than it does. Perhaps it has been subject to periodic climatic fluctuations, such as drought, that have reduced the mesophytes. Further exploration is likely to yield more endemics, yet some of those listed above may prove to be known elsewhere. The upland evergreen forest seems to be especially lacking in endemics, the *Polystachya* sp. nov. being the only one. In fact, it is the lowland that supports the endemics, this being especially true of the desert further east beyond Marsabit towards and beyond the Somali frontier. The ancient desert of Ogaden/Somalia appears to have been a centre of speciation unmatched elsewhere north of the Equator.

PROBLEMS OF DISPERSAL AND CONCLUSIONS

In considering problems of seed dispersal, especially of montane species, it is necessary to know how isolated is Mt Kulal in relation to other mountains in the vicinity. It lies c. 50 km north of Nyiru Mt, (2 752 m alt.); c. 110 km NW of the Ndotos (2 637 m alt.); c. 100 km W of Marsabit Mt (1 836 m alt.). Asie Hill lies only 20 km to the NE, but it is too low (1 070 m) to act as a stepping stone for montane plants. Likewise, the Hurri Hills (c. 100 km NE alongside the Ethiopian frontier) are not high enough (1 539 m) for forest, but do have upland grassland and a number of endemics.

The Afromontane species are therefore very discontinuous, as elsewhere in Africa (White, 1981).

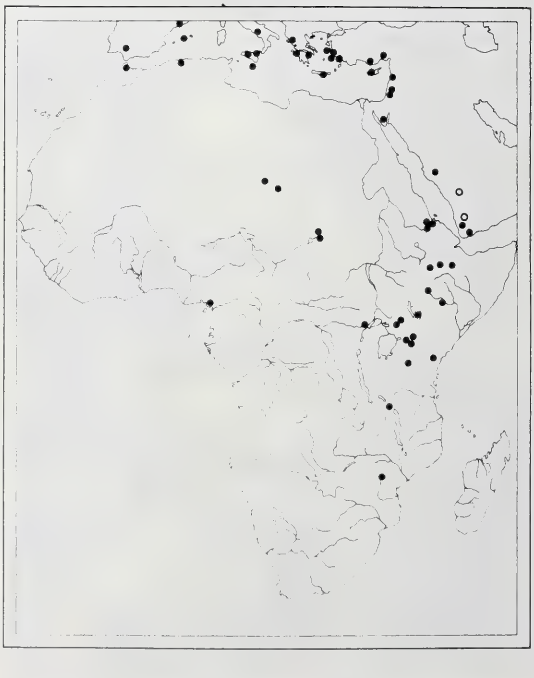

FIG. 13. Distribution of *Andropogon distachyos* — Afromontane Domain, extending to Mediterranean Region (from Wickens, 1976).

Some species such as *Halleria lucida* and *Myrsine africana* (Fig. 14) have an extremely wide distribution in tropical Africa and one wonders why this is so when other species are much more restricted. Wickens (1976) discussed long-range dispersal of seed of plants occurring on Jebel Marra and analysed the dispersal mechanisms of many species. It would be interesting to make a similar study of the Mt Kulal plants at all altitudes, but it is not practicable for this paper.

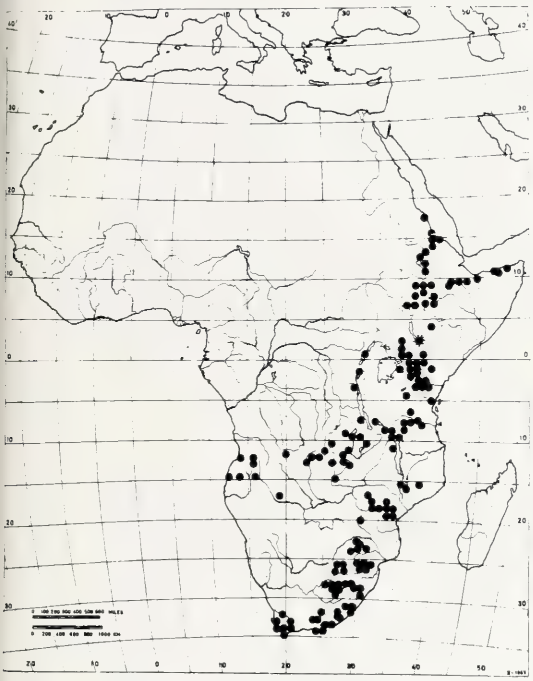

FIG. 14.—Distribution of *Myrsine africana* — Afromontane Domain, widespread in Africa (from White, 1981).

Species from the north have had to jump a considerable distance from the highlands of Ethiopia to Mt Kulal. However, there are so many species in common to both Ethiopia and the East African mountains that the desert of NE Kenya has not been a barrier. Gillett (1952) challenged the supposition then widely held that there was a gap between the highland floras of Ethiopia and E. Africa. Since the publication of his paper a great deal more knowledge of the floras has been acquired and his thesis is thoroughly vindicated.

The distances from the outlying mountains to the south are not so great. Until 1970's herds of elephants and other big game visited Mt Kulal and they were probably responsible for the distribution of certain plants. Birds are even more mobile, but Moreau (1963) has shown that many forest birds remain in relatively small areas on isolated mountains. Migrating birds, on the other hand, would be able to effect long distance seed dispersal. Much remains to be discovered about dispersal methods as well as the limitation of distribution owing to minimum/maximum temperatures, drought and the presence of pests. The effect of pests on the distribution of plants was first given prominence by Gillett (1962) whose ideas are now generally accepted.

Climatic changes have taken place which would have affected plant distribution across the region (Van Zinderen Bakker, 1967). Much of the low-level basalt is water-eroded, and evidence seems to indicate that even quite recently it was less dry in the plains. During such a wetter period there were sure to have been dispersal routes along numerous watercourses where riverine forest was likely to have developed. Temperature fluctuations would also affect distribution; a drop in temperature could have enabled some of the submontane species to spread across areas at present impassable. Distribution of desert species presents no problem as they can migrate eastwards or westwards with little difficulty. Floristically, however, there is a marked difference between the Marsabit District and Ogaden/Somali desert to the east — the much richer flora of the Ogaden is probably due to long stability of the environment there compared with fluctuations in the west involving volcanic activity.

CONCLUSION

In conclusion, the evidence favours Mt Kulal as a phytogeographical stepping stone between the highland mass of East Africa and Ethiopia, rather than an outlier of either of them.

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Phytogeography of African Commelinaceae

R. B. FADEN*

ABSTRACT

Africa (including Madagascar) has nearly twice as many species of Commelinaceae as any other continent (approximately 270 species, or about 40% of the total in the family). Of the 17 genera which are native, seven (*Anthericopsis, Coleotrype, Palisota, Polyspatha, Pseudoparis, Stanfieldiella* and *Triceratella*) are endemic, the highest percentage generic endemism of any continent. Within Africa generic diversity is slightly higher in western than in eastern tropical floras. Species richness, however, is greatest in eastern Africa, mainly due to a high diversity of species of *Commelina* and *Aneilema.*

Africa shares more genera with Asia (nine) than with any other continent. Only one African genus, *Buforrestia,* is neither endemic nor shared with Asia. Its western African/northeastern South American distribution is unique in the family. Besides *Buforrestia,* only five other genera of Commelinaceae (out of a total of 50 in the family), occur in both the Old and New Worlds. These genera, *Aneilema, Commelina, Floscopa, Murdannia* and *Pollia* are all very widespread in the Old World, occurring in Australia and Asia in addition to Africa (both continental and Madagascar).

Madagascar is relatively poor in species (31), but these include the endemic Madagascan genus *Pseudoparis,* the sole African species of *Rhopalephora*, and the largest number of species of the Afro-Malagasy endemic genus *Coleotrype.*

The high rate of generic endemism of Commelinaceae in Africa probably indicates that Africa was one of the ancient centres of diversity for the family. The high species diversity is more likely due to relatively recent radiations by genera pre-adapted to survival in non-forest habitats. The occurrence of only a small number of genera on both sides of the Atlantic suggests that the Commelinaceae have been evolving independently in the eastern and western hemispheres for a long period.

RÉSUMÉ

PHYTOGÉOGRAPHIE DES COMMÉLINACÉES AFRICAINES

L'Afrique (y compris Madagascar) a presque deux fois plus d'espèces de Commelinaceae que n'importe quel autre continent (approximativement 270 espèces ou environ 40% du total de la famille). Des 17 genres qui sont indigènes, sept (Anthericopsis, Coleotrype, Palisota, Polyspatha, Pseudoparis, Stanfieldiella *et* Triceratella) *sont endémiques; c'est le pourcentage d'endémisme générique le plus élevé de tous les continent. En Afrique la diversité générique est légèrement plus élevée dans les flores tropicales de l'Ouest que dans celles de l'Est. La richesse en espèces est cependant plus grande en Afrique orientale par suite d'une diversité élevée des espèces de* Commelina *et d'*Aneilema.

L'Afrique a plus de genres en commun avec l'Asie (neuf) qu'avec n'importe quel autre continent. Seul un genre africain, Buforrestia, *n'est ni endémique ni commun avec l'Asie. Sa distribution en Afrique occidentale et au Nord-Est de l'Amérique du Sud est unique dans la famille. A part* Buforrestia, *cinq autres genres seulement de Commelinaceae (sur un total de 50 dans la famille) se rencontrent à la fois dans l'Ancien et le Nouveau Mondes. Ces genres,* Aneilema, Commelina, Floscopa, Murdannia *et* Pollia, *sont tous très largement répandus dans l'Ancien Monde, se trouvant en Asie et en Australie en plus de l'Afrique (continentale et Madagascar). Madagascar est relativement pauvre en espèces (31) mais celles-ci comprennent le genre endémique malgache,* Pseudoparis, *la seule espèce africaine de* Rhopalephora *et le plus grand nombre d'espèces de genre endémique Afro-Malgache,* Coleotrype.

Le niveau élevé d'endémisme générique de Commelinaceae en Afrique, indique probablement que l'Afrique fut un des anciens centres de diversité pour la famille. La diversité élevée d'espèces est très vraisemblablement due à des radiations relativement récentes par des genres pré-adaptés à la survivance en habitats non forestiers. L'occurence de seulement un petit nombre de genres sur les deux cotés de l'Atlantique suggère que les Commelinaceae ont évolué indépendamment dans les hémisphères Est et Ouest pour une longue période.

INTRODUCTION

The Commelinaceae are the fifth largest family of monocotyledons in tropical Africa (after the Poaceae, Orchidaceae, Cyperaceae and Liliaceae). The family is virtually absent from temperate and Saharan Africa, but it is widely distributed in all tropical parts of the continent (Table 1). Africa (including Madagascar) has, with approximately 270 species (40% of the family), in 17 genera, nearly twice as many species of Commelinaceae as any other continent. Accompanying this species richness there is a high degree of generic and specific endemism. In the following account, the distribution of each African genus is summarized briefly. In the discussion distribution patterns in Africa for the family as a whole and the phytogeographic relationships of the African Commelinaceae are considered.

GENERIC CONCEPTS

Generic concepts within the Commelinaceae are presently in a state of flux, particularly for the New World genera. The generic concepts for the Old World genera used here differ from those of Brenan (1966) in that *Dictyospermum, Tricarpelema* and *Rhopalephora* are treated as distinct from *Aneilema* (see Faden, 1975; 1977); *Ballya* is included in

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TABLE 1.—Distribution of Commelinaceae in Africa by floral region

Genus	W.T.A.*	Cameroun	Gabon	Afrique Centrale	Angola	S.W.A.	Southern Africa	Zambesiaca	T.E.A.	Ethiopia & Somalia	Madagascar	Total African species
Amischotolype	1**	1	1	1	–	–	–	–	–	–	–	1
Aneilema	10	6	3	12	6	2	10	22	37	18	1	56
Anthericopsis	–	–	–	1	–	–	–	1	1	1	–	1
Buforrestia	2	1	–	–	–	–	–	–	–	–	–	2
Coleotrype	1	–	–	1	–	–	1	1	2	–	6	9
Commelina	24	+	+	+	+	10	+	+	c. 60	+	c. 13	c. 125
Cyanotis	11	+	+	+	+	3	+	+	11	+	2	c. 20
Floscopa	10	+	+	+	+	1	1	+	7	1	1	c. 16
Murdannia	3	2	1	4	2	1	1	3	5	1	3	11
Palisota	9	+	+	+	1	–	–	1	4	–	–	c. 15
Pollia	2	2	+	+	1	–	–	–	3	2	1	4
Polyspatha	2	2	+	+	1	–	–	–	2	–	–	2
Pseudoparis	–	–	–	–	–	–	–	–	–	–	2	2
Rhopalephora	–	–	–	–	–	–	–	–	–	–	1	1
Stanfieldiella	4	3	1	1	1	–	–	–	1	1	–	4
Tricarpelema	–	1	–	–	–	–	–	–	–	–	–	1
Triceratella	–	–	–	–	–	–	–	1	–	–	–	1
Total species	79	–	–	–	–	17	–	–	c. 133	–	c. 30	c. 271
Total genera	12	12	10	12	9	5	6	9	11	8	9	17
Endemic African genera	4	3	3	5	3	0	1	4	5	2	2	7

*Geographic regions as defined in the following floras: Flora of West Tropical Africa, ed. 2; Flore du Cameroun; Flore du Gabon; Flore d'Afrique Centrale (= Flore du Congo Belge et du Ruanda-Urundi; = Flore du Congo, du Rwanda et du Burundi); Conspectus Florae Angolensis; Prodromus einer Flora von Südwest-afrika; Flora of Southern Africa; Flora Zambesiaca; Flora of Tropical East Africa; Adumbratio Florae Aethiopicae; Flore de Madagascar et des Comores.

** Numbers of species present are listed where known (based on published records, herbarium specimens, etc.). Otherwise presence (+) or absence (–) of the genus is indicated.

Aneilema (Faden, 1975); *Aclisia* is included in *Pollia* (Faden, 1975; Faden & Suda, 1980); and *Porandra* (Hong, 1974) is recognized as doubtfully distinct from *Amischotolype.* For the New World genera the differences from Brenan (1966) are as follows: *Setcreasea* and *Separotheca* are included in *Tradescantia,* following Hunt (1975); *Cuthbertia* is considered distinct from *Phyodina;* and the new genera *Elasis, Gibasoides* and *Matudanthus* (Hunt, 1978) are accepted. A soon to be described genus related to *Geogenanthus,* ranging from Panama to Peru, is included in the total of 51 genera recognized for this treatment.

DISTRIBUTION OF GENERA

Amischotolype

Amischotolype (syn. *Forrestia* A. Rich.) is represented in Africa by a single western African species, *A. tenuis* (C. B. Clarke) Rolla Rao (Nigeria to Zaire). The 10–15 other species in the genus range from north-eastern India to New Guinea.

Aneilema

Fifty-six of the 62 species of *Aneilema* occur in Africa (Faden, 1975, and unpublished). Two of the African species, *A. umbrosum* (Vahl) Kunth and *A. forskalii* Kunth extend to tropical America and the Arabian Peninsula, respectively. Of the remaining six species, one (underscribed) is endemic to the Yemen Arab Republic and the other five to Australia and the surrounding islands including New Guinea.

Within Africa the principal centre of taxonomic and morphological diversity of *Aneilema* is in eastern and north-eastern Africa; from southern Ethiopia and central Somali Republic south to central Tanzania. Secondary concentrations of taxa occur in the miombo region of south-western Tanzania and adjacent Zambia and Zaire; from southern Mozambique and south-western Zimbabwe to northern and eastern Transvaal and the north-eastern Cape Province of South Africa; and in the savannah region of West Africa; Sierra Leone and Senegal to Nigeria (Faden, 1975). The single Madagascan species, the endemic *A. aparine* Perrier, is the sole African species of section *Aneilema* which otherwise includes all of the Australian region taxa.

Anthericopsis

The sole species of this endemic African genus, *A. sepalosa* (C. B. Clarke) Engl., ranges from Ethiopia to Malawi and Zaire.

Buforrestia

The two African species of *Buforrestia* are endemic and allopatric: *B. mannii* C. B. Clarke from Nigeria to Cameroun and *B. obovata* Brenan from Guinea to Ghana (Brenan, 1968). The third species, *B. candolleana* C. B. Clarke, is South American and stretches from Surinam to north-eastern Brazil.

Coleotrype

Coleotrype, a genus of 9 species, plus many infraspecific taxa described from Madagascar, is the only endemic African genus of *Commelinaceae* which occurs both on Madagascar (six species) and on the mainland (three species). Perrier (1936; 1938) informally separated the Madagascan taxa from the continental species. He compared only *C. natalensis* C. B. Clarke on the basis of corolla and androecial morphology, a distinction which appears to be sound. The three mainland species are allopatric: *Coleotrype natalensis* (South Africa to Mozambique and Zimbabwe); *C. bruecknerana* Mildbr. (eastern Kenya and Tanzania); and *C. laurentii* K. Schum. (West Africa to Uganda).

Commelina

The nearly cosmopolitan genus *Commelina* is the largest in the family, with about 170 species. It is best developed in Africa where approximately 125 species, many still undescribed, occur. All but about 11 of the African species are endemic to the continent and/or Madagascar. Within Africa, *Commelina* has its greatest number of species in the *Flora of Tropical East Africa* and *Flora Zambesiaca* areas. It is especially diverse in the miombo areas of southern Tanzania, northern Zambia and south-eastern Zaire.

Cyanotis

About 20 of the approximately 45 species of *Cyanotis* occur in Africa. The remainder are mainly Asiatic. India is the centre of taxonomic diversity, but one species, *C. axillaris* (L.) Sweet, extends to northern Australia. The genus as used here includes *Amischophacelus* Rao Rolla & Kammathy (see Faden & Suda, 1980). The African species are more or less evenly distributed except for the forested areas where they are rare or lacking. The species in West Africa include a high proportion of local endemics (Brenan, 1968), whereas the species in Tropical East Africa are mostly widespread (Faden, unpublished). Five of the African species also occur outside of Africa.

Floscopa

Floscopa, with about 20 species, is a mainly African genus. A single species, according to all recent treatments, *F. scandens* Lour., ranges from India and Sri Lanka to Australia. A group of about four species occurs in South America with one of them, *F. robusta* (Seub.) C. B. Clarke, extending north to Nicaragua. All of the African species have generally been considered endemic, but the South American *F. glabrata* (Kunth) Hassk. may prove conspecific with the African *F. confusa* Brenan. Within Africa *Floscopa* is most diverse in West Africa, and only the most widespread African species, *F. glomerata* (J. A. & J. H. Schult.) Hassk., reaches Ethiopia, Kenya, South Africa and Madagascar.

Murdannia

Murdannia, a pantropical but principally Asiatic genus of about 50 species, has 11 taxa in Africa of which seven (or perhaps six) are endemic. The only questionable endemic is *M. axillaris* Brenan of the East African coast which is uncomfortably close to certain collections of the Asiatic *M. blumei* (Hassk.) Brenan.

Except for *M. simplex* (Vahl) Brenan and *M. tenuissima* (A. Chev.) Brenan, most African species are rather local. There is no concentration of species in any part of the continent. In Africa, *M. gigantea* (Vahl) Brückn. is restricted to Madagascar.

Palisota

With about 15 species (variously estimated up to 25 species: Morton, 1967; Willis, 1973) *Palisota* is the largest endemic African genus of Commelinaceae. Its centre of diversity is western Africa, especially Cameroun, but species occur as far east as the mountains of eastern Tanzania. The genus is present on the islands of the Gulf of Guinea but it is absent from Madagascar and the Indian Ocean islands.

Pollia

The four African species of *Pollia,* a mainly paleotropical genus of about 17 species, are all endemic: *P. gracilis* C. B. Clarke (Madagascar, Comoro Islands); *P. bracteosa* K. Schum. (Uluguru Mountains, Tanzania); *P. mannii* C. B. Clarke (widespread in West Africa east to Ethiopia, Uganda and Tanzania); *P. condensata* C. B. Clarke (widespread in West Africa east to eastern Tanzania). *Pollia sambiranensis* Perrier of Madagascar is a species of *Aneilema.* The genus was recently discovered in the New World (Faden, 1978).

Polyspatha

The two species of this endemic African genus, *Polyspatha paniculata* Benth. and *P. hirsuta* Mildbr., are widespread in western Africa (Sierra Leone to Angola), extending east to Uganda (Brenan, 1968).

Pseudoparis

Pseudoparis, with two described species, *P. monandra* Perrier and *P. cauliflora* Perrier, is the only genus of Commelinaceae which is confined to Madagascar.

Rhopalephora

The single African species of this genus is the endemic Madagascan *R. rugosa* (Perrier) Faden. The three other species range from India and Sri Lanka to the Fiji Islands (Faden, 1977).

Stanfieldiella

The six taxa (four species plus two varieties) of the African endemic genus *Stanfieldiella* are nearly restricted to West Africa (Brenan, 1960, 1968). Only *S. imperforata* (C. B. Clarke) Brenan extends further east (to eastern Tanzania) or south (to Angola) of Cameroun.

Tricarpelema

This genus was collected in Africa for the first time in 1964. The species, which will be described elsewhere, was gathered at N'Kolbisson, Cameroun *(De Wilde et al.* 3728, BR, K, WAG) and, to this author's knowledge, it has not been recollected. The remaining six species of the genus (as used in the sense of *Dictyospermum* subgen. *Tricarpelema* of Faden, 1975) are Asiatic, ranging from northeastern India to the Philippines and Borneo.

Triceratella

This morphologically eccentric, monotypic, African endemic genus is known from a single collection made in Zimbabwe in 1958 (Brenan, 1961).

DISCUSSION

The distributions of the African genera of Commelinaceae have been outlined above and are summarized in Table 1. Several generalizations may be made. The largest genera, except *Palisota*, are the most widely distributed. The five genera which occur in all eleven African floral regions, *Aneilema*, *Commelina*, *Cyanotis*, *Floscopa* and *Murdannia* are also widespread outside of Africa, occurring in Asia, Australia and, except *Cyanotis*, South and North America. These five genera include 228 African species or about 84% of the total species in the continent and Madagascar.

Significantly, all five of these genera comprise species principally of non-forest habitats. Among the remaining 12 genera only the monotypic African endemics *Anthericopsis* and *Triceratella* could be characterized as non-forest genera. Five of the 10 forest genera are endemic. Three of these endemic genera, *Palisota*, *Polyspatha* and *Stanfieldiella*, have their centres of diversity in western Africa; a fourth, *Pseudoparis*, is confined to Madagascar; and the fifth, *Coleotrype*, is most diverse in Madagascar, but is also scattered on the continent. Of the five non-endemic forest genera, the African species of *Amischotolype*, *Buforrestia* and *Tricarpelema* are restricted to western Africa; *Rhopalephora* occurs only in Madagascar; and only *Pollia* could be described as widespread: it is the sole forest genus in the family to occur in Asia, Australia and the New World, in addition to Africa.

The preponderance of forest genera in western Africa and Madagascar is a distribution pattern that is prevalent in many groups of flowering plants as well as in pteridophytes. This pattern is undoubtedly relictual, being the result of the increasing aridity in Africa during the Neogene and again since the late Pleistocene (Axelrod & Raven, 1978; Richardson & Richardson, 1972). This desiccation was in part associated with the onset of the formation of the Rift Valley system, and hence it was most severe in eastern Africa. Lowland forest taxa tended to become isolated in western Africa and Madagascar where climatic deterioration was less intense. Some taxa also survived in isolated coastal and subcoastal forests of eastern Africa, sometimes with subsequent morphological differentiation (Faden, 1973).

The occurrence of western African forest taxa or clear relatives thereof in these East African forests provides strong evidence that these genera and, by inference, others were once more widespread in the continent. In the Commelinaceae three species span the gap of 650–850 km of unsuitable habitat: *Palisota schweinfurthii* C. B. Clarke, *Pollia condensata* C. B. Clarke, and *Stanfieldiella imperforata* (C. B. Clarke) Brenan. Three genera are represented by vicariant forest species in the two areas: *Coleotrype* by *C. laurentii* K. Schum. in western Africa (east to Uganda) and *C. bruecknerana* Mildbr. in eastern Kenya and Tanzania; *Palisota* by *P. ambigua* (P. Beauv.) C. B. Clarke in western Africa and *P. orientalis* K. Schum. in eastern Tanzania; and *Aneilema* by *A. beniniense* (P. Beauv.) Kunth in western Africa and *A. dispermum* Brenan in eastern Tanzania and Malawi. I do not regard the West African plants treated as *A. disperum* (Brenan, 1968) as conspecific with the East African plants.

The increasing aridity in Africa during the Neogene led to a great increase in drier habitats, ranging from woodland to semidesert. This would have provided non-forest genera ample opportunities to diversify and speciate. The major radiations of *Commelina* and *Aneilema*, which are apparently still ongoing, probably began during this period. Therefore whereas the reduction of lowland rainforests in the Miocene may have decreased diversity among the forest genera of Commelinaceae, possibly leading to the extinction of some, its overall effect would probably have been to have greatly increased the total number of species in the family.

Phytogeographically the African Commelinaceae are most closely related to those of Asia (including Malesia). Nine of the ten nonendemic African genera — all but *Buforrestia* — also occur in Asia (vs. six in Australia and five each in North and South America). Three of those nine genera, *Amischotolype*, *Rhopalephora* and *Tricarpelema*, are restricted to these continents. Of the 23 African species (8% of the total), which are not endemic to the continent or Madagascar, 22 also occur in Asia (all but *Aneilema umbrosum*). No doubt the floristic similarity between Africa and Asia can be accounted for in part by the present direct land connection between the two continents. In a future paper the effects of the altering positions of the continents during the Tertiary will be considered.

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Geography of Iridaceae in Africa

P. GOLDBLATT*

ABSTRACT

Iridaceae, a family of worldwide distribution, comprises some 1 500 species and 85 genera. It exhibits its greatest radiation in Sub-Saharan Africa, where over half the species and some 48 genera occur, 45 of which are endemic. All three major subfamilial taxa are represented in Africa, where Ixioideae are almost entirely restricted, with extensions into Eurasia. Areas of greatest concentration are either montane or in areas of winter rainfall. In southern Africa alone, there are some 850 species in 46 genera, making the family the fifth largest in the flora. In the Cape Floristic Region there are 620 species, and the family is the fourth largest in this area. All major infrafamilial groups occur in the Cape Region where most of the variability as well as generic radiation is encountered. The idea of a southern origin for Iridaceae in Africa is analysed systematically, and is correlated with the major climatic changes that occurred in Africa since the mid-Tertiary, and culminated in the seasonally dry climates along the west coast. The establishment of mediterranean climate in the southwest provided the stimulus for massive speciation and radiation of the family there. Plio-Pleistocene uplift along the eastern half of the African continent led to the establishment of substantial upland areas and allowed the spread of some genera, such as *Romulea, Gladiolus, Moraea,* and *Hesperantha* into tropical Africa. Short-distance dispersal probably accounts for the presence of genera such as *Gladiolus, Gynandriris* and *Romulea* in Eurasia.

RÉSUMÉ

GÉOGRAPHIE DES IRIDACEAE EN AFRIQUE

Les Iridaceae, famille répandue dans le monde entier, comprend quelques 1500 espèces et 85 genres. Elle présente sa plus grande expansion en Afrique au sud du Sahara où plus de la moitié des espèces et quelques 48 genres sont présentes, 45 d'entre eux étant endémiques. Les trois sous-familles principales sont représentées en Afrique, où les Ixioideae s'y limitent presqu'entièrement avec des extensions en Eurasie. Les régions aux plus grandes concentrations sont soit montagnardes soit en région à pluies hivernales. En Afrique australe seule, il y a quelques 850 espèces et 46 genres, faisant de cette famille la cinquième plus grande de la flora. Dans la Région floristique du Cap, il y a 620 espèces et la famille est la quatrième en importance de cette région. Tous les groupes majeurs infra-familiaux existent dans la région du Cap où le plus de variabilité et radiation générique sont rencontrées. L'idée d'une origine australe pour les Iridaceae en Afrique est analysée systématiquement et est mise en corrélation avec les changements climatiques qui survinrent en Afrique depuis le milieu du Tertiaire et qui culminèrent dans le climats saisonnièrement secs, le long de la côte de l'Ouest. L'établissement d'un climat méditerranéen dans le Sud-Ouest a fourni le stimulus de la spéciation et de l'expansion massive de la famille à cet endroit. Le soulèvement Plio-Pleistocène le long de la moitié orientale du continent africain amena l'établissement de régions élevées assez importantes et permit la dissémination de certains genres tels que Romulea, Gladiolus, Moraea *et* Hesperantha *en Afrique tropicale. Une dispersion à courte distance explique probablement la présence des genres tels que* Gladiolus, Gynandriris *et* Romulea *en Eurasie.*

INTRODUCTION

Iridaceae are a family of petaloid monocotyledons, of the order Liliales, comprising some 1 500 species in 85 genera, distributed throughout the world. The area of greatest concentration is Africa south of the Sahara, where ca. 48 genera and about 925 species occur. Explosive radiation has taken place in the extreme southwestern part of the continent, an area of mediterranean climate. In this Cape Floristic Region there are 620 species in 36 genera (Goldblatt, 1978). Iridaceae is the fifth largest family in southern Africa in terms of numbers of species and fourth largest in the Cape Region, a situation without parallel for a petaloid monocot group.

Outside the Cape Region and the immediately adjacent western Karoo and Namaqualand, significant numbers of species occur in the well watered coastal and mountain belts of eastern southern Africa. North of the Transvaal, species of Iridaceae are concentrated in the islands of Afromontane flora that extend northwards through Zimbabwe, Malawi, Tanzania and Kenya into Ethiopia. Smaller numbers of species occur in savanna regions. Very few occur in lowland forest.

The general pattern of the distribution of Iridaceae suggests an explosive radiation in the Cape Region with secondary migration and dispersal from this area eastwards and then northwards; species numbers decreasing with latitude. This implies a southern (and thus Cape) origin for the family in Africa. The situation is, however, more complex and can only be interpreted from post-Cretaceous climatic changes that have occurred in Africa. Since the Eocene (55–38 m.y. ago), when the ancestors of the modern genera of Iridaceae were found in Africa and South America (and probably Australasia), the African continent has moved some 15° northwards (Axelrod & Raven, 1978). At the same time, climates became warmer, drier and more strongly seasonal. After the Miocene, dry zones began to develop, culminating in the establishment of a mediterranean climate along the southwest coast and desert to the north and east.

ECOLOGY OF IRIDACEAE

Species of Iridaceae are almost exclusively herbaceous perennials; a few are annual or shrubby. The majority are adapted to climates with a

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substantial dry season. This is particularly so in Africa, where adaptations for seasonal climates such as deciduous habit, specialized underground organs, and reduced plant size are found in the majority of species, including all of the more advanced lines.

A few, mostly primitive and probably very old, genera occur either in association with evergreen forest (notably *Dietes* and *Aristea*), in grassland in areas of high rainfall (*Dierama*), or in favourable habitats in areas of apparently arid climate. Such habitats include stream sides, or sheltered valleys and ravines in mountainous areas, where dry season moisture is available through cloud condensation. Therefore, although the arid, summer-dry climate of the Cape Region is of comparatively recent origin, and much of the species richness is equally recent, local areas of moist climate here harbour species not at all drought adapted. Such species are often isolated relics (*Pillansia, Aristea* spp., and *Bobartia*). These genera, together with the few forest or moist grassland genera provide important clues to the origin and evolution of Iridaceae in Africa. Before analysing them further, however, the systematic classification of Iridaceae is outlined.

IRIDACEAE — OUTLINE OF CLASSIFICATION AND REVIEW OF MODERN DISTRIBUTIONS OF GENERA

Iridaceae are usually treated as comprising three major infrafamilial groups, which for convenience, are best regarded as subfamilies. These are the Ixioideae, Iridoideae and Sisyrinchioideae. There is some doubt about the status and circumscription of the latter, but it is useful for purpose of this paper to recognize it.

(a)*Sisyrinchioideae.* This predominantly New World subfamily is represented on all southern continents. It is fairly low on the evolutionary scale: representatives typically have unspecialized flowers and unmodified underground parts. There are five African genera (Table 1). *Aristea,* the largest, together with *Klattia, Witsenia* and *Nivenia* form one alliance, and *Bobartia* another. The less specialized species of *Aristea* occur in well watered grassland throughout Africa and Madagascar (Weimarck, 1940) and also in moist sites in the south-western Cape. More specialized species, belonging to several alliances are restricted to the Cape Floristic Region, where some recent radiation seems to have occurred. The peculiar shrubby genera, *Klattia, Witsenia* and *Nivenia* are found exclusively in the mountains of the Cape Region, mostly in more favoured situations. All are very specialized in their shrubby habit and also in their flowers. The group probably represents a unique trend in Iridaceae towards the shrubby growth form very common in the Cape Region, although rare in monocots.

Bobartia, distantly related, if at all, to the *Aristea* group, is usually regarded as most closely allied to the New World *Sisyrinchium.* If this is correct, the separation must be very ancient. The affinities of *Bobartia* are by no means satisfactorily understood and require investigation. *Bobartia* may possibly be an abberant member of Iridoideae (Goldblatt, 1979) rather than a member of Sisyrinchioideae.

The genus consists of 15 species. Two, with a presumably primitive open branching pattern, occur at high altitudes in the mountains of the Cape Region. The 13 more specialized species, with clustered inflorescenses and lacking branches, extend from the western Cape to southern Natal. They probably represent recent speciation in an old group.

(b)*Iridoideae.* All African Iridoideae belong to the Old World tribe Irideae, the sister group of the New World Tigridieae. The most primitive genus of Irideae is *Dietes* (Goldblatt, 1981), with six species. Five occur in Africa, from Kenya to the southern Cape, and one is restricted to Lord Howe Island (Australasia). All species occur in forest or streamside habitats, are evergreen, and have unspecialized flowers for the tribe. *Dietes* or something very like it, probably gave rise to the two important lines of the Old World Irideae, *Iris, Hermodactylis, Pardanthopsis, Belamcanda,* etc. (Iridinae) in Eurasia (*Iris* extending to North America) and *Moraea,* its allies (Homeriinae) and *Ferraria* (Ferrariinae) in Africa. Most African members of Irideae are strongly drought adapted, are deciduous, have cormous rootstocks and with the exception of the isolated *Ferraria,* have an unusual bifacial type of leaf (Goldblatt, 1976).

The group has radiated considerably in the Cape region (Table 1) and adjacent Namaqualand, where several genera are endemic. *Moraea,* the largest genus extends into tropical Africa, where two specialized subgenera have become established, and *Ferraria,* mainly West Coast, has its most primitive species in central Africa. One specialized offshoot of *Moraea, Gynandriris* (Goldblatt, 1980) is centred in southern Africa, but two species are endemic in Eurasia, both polyploid and probably of recent origin there.

(c)*Ixioideae.* This subfamily, the largest in the family in Africa, consists of several separate lines, the relationships of which are not understood (Goldblatt, 1971). It is predominantly African. All 34 genera, except *Crocus,* occur in Africa south of the Sahara, and only *Gladiolus* and *Romulea,* both centred in the Cape Region, occur north of the Sahara.

Only three genera of significance do not occur at all in the Cape Region. Two, *Savannosiphon* (1 sp.) (Goldblatt & Marais, 1979) and *Zygotritonia* (2 spp.) are apparently isolated taxonomically, and possibly relictual, but seem fairly specialized. The third *Dierama* (ca. 15 spp.) is centred in the well watered coastal and montane grassland of eastern southern Africa. It extends north to Ethiopia (Cufodontis, 1974), occurring only in mountain areas. Most species are evergreen, and all have unspecialized actinomorphic flowers. Lewis (1962) regarded the predominantly Cape genus *Ixia* as closely allied to *Dierama,* but differing mainly in being deciduous, and having seasonally produced corms.

Apart from this example (and possibly also the *Crocosmia-Tritonia* alliance) all Ixioid lines are centred in the Cape Region. This is where most

TABLE 1.—Genera of African Iridaceae occurring south of the Sahara, with number of species in parentheses, and range. Notable disjunctions are highlighted in italics

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Sisyrinchioideae

Aristea (50) SW Cape–Ethiopia incl. Madagascar
Klattia (2) southern Cape mts
Witsenia (1) southern Cape–marshes
Nivenia (8) Cape, mainly montane
Bobartia (15) Cape–S Natal

Iridoideae

Dietes (6) Africa, S Cape–Kenya and *Lord Howe Island*
Moraea (ca. 102) Africa, Cape–Ethiopia
Homeria (31) Cape–Namaqualand and Karoo to E Transvaal
Ferraria (10) SW Cape and Namaqualand–*Katanga*
Barnardiella (1) Namaqualand
Gynandriris (9) Cape–Karoo and *Eurasia* (2)
Roggeveldia (1) W Karoo
Rheome (2) W Cape
Hexaglottis (5) Cape–Namaqualand
Galaxia (13) Cape–Namaqualand

Ixioideae

Pillansia (1) SW Cape
Watsonia (70) SW Cape–eastern Transvaal Mts
Micranthus (3) SW Cape
Therianthus (7) SW Cape
Lapeirousia (28) SW Cape–Namaqualand–Ethiopia
Savannosiphon (1) SE tropical African plateau
Romulea (ca. 90) Cape and Namaqualand eastwards through Drakensberg and East African Highlands to Ethiopia (ca. 80) and *Mediterranean, Canary Islands* (ca. 15)
Syringodea (8) Cape–Karoo
Anomatheca (5) Cape and Namaqualand through E Cape to southern Tanzania
Freesia (11) Cape and Karoo (to southern Transkei)
Dierama (ca. 15) E Cape–Kenya, montane grassland, coastal in south
Ixia (45) SW Cape to Namaqualand
Sparaxis (6) W Cape
Synnotia (6) W Cape
Tritonia (ca. 30) SW Cape and Namaqualand through E Cape to Zimbabwe
Crocosmia (6) E Cape–Tanzania
Chasmanthe (3) SW Cape
Duthieastrum (1) N Cape–W Transvaal
Gladiolus (160) SW Cape and Namaqualand, throughout tropical Africa and Madagascar in mountains and savannas (145) also in *Eurasia* (15)
Homoglossum (10) SW Cape
Anomalesia (3) SW Cape to Namibia
Radinosiphon (?1) E Transvaal to Zambia, along the escarpment
Oenostachys (?6) South tropical Africa to Ethiopia, mainly high mountains
Hesperantha (50) SW Cape and Namaqualand through E Cape to Ethiopia
Schizostylis (1) Transkei to Zimbabwe
Geissorhiza (70) SW Cape and Namaqualand
Engysiphon (8) SW Cape (to Geissorhiza)
Melasphaerula (1) SW Cape and Namaqualand
Tritoniopsis (14) SW Cape
Anapalina (7) SW Cape–Transkei
Babiana (63) SW Cape and Namaqualand, Karoo to Zimbabwe (62) and *Socotra* (1)
Antholyza (2) SW Cape and Namaqualand
Zygotritonia (2) tropical African savannas

variation occurs, the most primitive and presumably basal stocks are found, and much of the radiation and speciation has taken place. As in *Moraea* (Iridoideae), some genera have extended their range eastwards to some extent (*Anapalina, Watsonia*) into the well watered parts of southern Africa, or even into tropical Africa (*Gladiolus, Romulea, Hesperantha*), again mostly confined to mountain belts (Table 2). *Gladiolus* is exceptional in occurring in drier savannas as well, and it has spread, probably by short distance dispersal, into Eurasia, as has *Romulea*.

A few genera, also apparently centred, or at least well represented in the Cape Region, but adapted to drier habitats appear to have spread not eastwards through grassland, but northwards along the West Coast into the dry savanna and steppe of the Karoo-Namib zone. *Lapeirousia* is an outstanding example. Species of the *L. erythrantha* complex extend as far north as Nigeria and *L. abyssinica* and *L. schimperi* occur in Ethiopia (Cufodontis, 1974). The pattern in *Babiana* is similar, but most species occur in Namaqualand and the Karoo. Only *B. hypogea* reaches Zimbabwe and Namibia, and *B. socotrana* is disjunct on Socotra (Lewis, 1959). This disjunction seems unusual, but has parallels in several African plant families (De Winter, 1971).

Among the remaining non-Cape Ixioid genera are *Oenostachys, Schizostylis* and *Duthieastrum*. *Oenostachys* is a minor and possibly heterogeneous assemblage segregated from *Gladiolus; Schizostylis* is a semi-aquatic and possibly secondarily rhizomatous segregate of *Hesperantha* (Goldblatt, 1971); and *Duthieastrum*, monotypic, is probably a close ally of *Tritonia* found in the north-western Cape and western Transvaal.

DISCUSSION

The patterns of distribution for African genera of Iridaceae, as outlined, fall into four broad categories:

1. Occurrence of unspecialized genera in forests, forest margins and other well watered habitats (*Aristea, Dietes, Dierama*).
2. Restriction of unspecialized or moderately specialized small genera, mainly taxonomically isolated, to moist sites in the Cape Region (*Bobartia, Pillansia*).
3. Explosive radiation and speciation in moderately to highly specialized genera within the Cape Region (e.g. *Gladiolus, Geissorhiza, Ixia, Homeria;* also of derived species of some unspecialized genera) and the evolution of a few small specialized, bird pollinated genera here (*Homoglossum, Antholyza, Anapalina*).
4. Dispersal of representatives of some specialized Cape genera either northeast into well watered and climatically mild parts of south tropical and east tropical Africa along mountain belts (*Gladiolus, Moraea, Hesperantha*) or northwest into the arid, climatically extreme Karoo-Namib and thence into tropical central Africa (*Babiana, Lapeirousia*).

TABLE 2. — Genera of Iridaceae with a pronounced centre in the Cape Region

1. Endemics or near endemics (locally extending into the western Karoo, Namaqualand or E Cape)

Klattia
Witsenia
Nivenia
Roggeveldia
Hexaglottis
Rheome
Galaxia
Pillansia
Micranthus
Thereianthus
Ixia
Sparaxis
Synnotia
Chasmanthe
Homoglossum
Geissorhiza
Engysiphon
Melasphaerula
Tritoniopsis
Antholyza

2. Genera with significant representation northeastwards (as far as Ethiopia, or Eurasia)

Bobartia (to Natal)
Moraea (to Ethiopia)
Watsonia (to Transvaal)
Romulea (to Eurasia)
Anomatheca (to Tanzania)
Tritonia-Crocosmia (to Ethiopia)
Gladiolus (to Eurasia)
Hesperantha (to Ethiopia)
Anapalina (to Transkei)

3. Genera with representatives extending north or west into arid zones (secondarily in tropical East Africa or Eurasia)

Gynandriris (to Karoo and Transvaal, and Eurasia)
Anomalesia (to Namibia through W Karoo and Namaqualand)
Babiana (to south central Africa and Socotra)

Note: Lapeirousia, though more diverse in the Cape area (Goldblatt 1972), has radiated in Namaqualand-Namibia, and as well in tropical Africa, and it cannot be regarded as a Cape genus. More information on primitive and advanced characters in *Lapeirousia* is needed before properly assessing its relationships and geography.

Ferraria has most of its species along the W Coast from the Cape, north to S Namibia, but the most primitive species is in central southern Africa and it is not, in a strict sense, a Cape genus.

The first pattern represents the most ancient one for African Iridaceae, and probably dates back to the Eocene, when lowland evergreen forest covered much of southern Africa (Axelrod & Raven, 1978), then lying some 12−15° S of its present position. Iridaceae presumably occurred either in open, rocky sites or on the forest floor much as *Dietes* and some species of *Aristea* do today. The single non-African *Dietes, D. robinsoniana,* occurs on the equable Lord Howe Island, a continental fragment lying between New Zealand and Australia, also in forested habitats. The significance of this distribution pattern is unclear (Goldblatt, 1981), but is most likely very old, although it probably does not predate the separation of Australia-Antarctica from Africa and therefore may represent long distance dispersal, perhaps across a narrow Indian Ocean via India when this lay between Africa and Australasia in the Eocene (Axelrod & Raven, 1978).

The first important climatic change in Africa during the Tertiary took place in the late Eocene (38 m.y. ago) when Antarctica became partly glaciated and substantial sea-ice began to form (Axelrod, 1981). As the bottom water temperature dropped and upwelling began, a drier climate began to spread over the middle latitudes. During the Oligocene the separation of Antarctica and Australia occurred, the circum-Antarctic current was initiated, and seasonal aridity spread. In Africa this trend was strengthened as coastal uplift, most notable along the eastern coast, broke the pattern of low relief of the continent (Axelrod & Raven, 1978). The establishment of open, seasonally dry habitats that these climatic changes imply, created a new adaptive zone for plants. Such open dry conditions would have favoured adaptations towards geophytism and deciduousness.

Corm-bearing and partly deciduous Iridaceae probably evolved from evergreen, rhizomatous ancestors at this time in such open or semi-forested habitats, probably in what is now central Africa, but which then lay some 10° to the south. Southern Africa then had a cool, wet climate and was heavily forested (Axelrod & Raven, 1978; Coetzee, 1978).

In the Miocene (26−5 m.y. ago) as the African plate moved northwards comparatively rapidly (Axelrod, 1981), the East African rift valley systems began to develop. Antarctic glaciation increased and the ocean off the west coast as a result became substantially cooler so that the western part of the subcontinent became drier than the east which was elevated and so cooler and wetter. The lines leading to the modern generic groups in Ixioideae and Iridoideae must then have differentiated in the general area of southeast central Africa.

Probably by the end of the Miocene (5 m.y. ago) most of the genera found today were in existence. These Iridaceae probably could not survive in the tropical areas that were becoming rapidly drier and were displaced southwards. The family probably reached the Cape at this time, which by now was north of the main zone of westerlies, but had a more equable climate than the plains of south central Africa.

During the Pliocene-Quaternary the climate became more extreme and at this period a winter rainfall pattern probably became established in south-western Southern Africa. The high plains to the north became extremely seasonal and dry and cold in the winter. These changes resulted in the opening of a major adaptive zone in southern Africa and one into which geophytes including Iridaceae were supremely preadapted. The genera must have undergone explosive radiation in this new climate zone, as the older, more mesic flora contracted into small pockets of more equable climate or was eliminated.

The sporadic uplift round the southern African coasts most likely meant that mountains existed here since at least the late Miocene. The quartzitic sandstones of the Cape system are particularly resistant to erosion and elevated sandstone areas must have been present for long periods, with perhaps greater or smaller height differentials from time to time.

The presence of elevated areas with accompanying higher rainfall, suggest that even as the climate deteriorated and became more extreme some sites remained available to plants not adapted to seasonally dry conditions. It seems likely that such unspecialized genera as *Bobartia* and *Aristea* (Sisyrinchioideae) *Pillansia* (Ixioideae) are essentially relics which survived as a result. In both *Bobartia* and *Aristea* some radiation subsequently occurred and both have species well adapted to the mediterranean type climate that prevails in the Cape today, but significantly, both are poorly represented in the more extreme west than in the south where summer precipitation is not uncommon and the temperatures lower.

The extraordinary radiation in genera like *Gladiolus, Moraea, Geissorhiza, Ixia, Romulea, Homeria,* to mention only some, is probably a phenomenon of the recent past, when a true mediterranean climate had become established. Part of the richness is due to the varied environments found in the mountainous Cape Region, with its differences in climate, soil and rainfall forming a complex mosaic throughout the area. The richness of species is well known for areas of mediterranean climate (Raven & Axelrod, 1978), but the Cape Region is substantially richer than comparable areas. The reasons for this are not clear (Goldblatt, 1978). Axelrod (pers. comm.) has suggested that the fluctuating climates of the Pleistocene, well documented in the south-western Cape (Schalke, 1973), perhaps acted as a species pump and that with each major climate shift new species evolved, while those already in existence migrated locally into sites suitable for their survival.

The evolution of bird-pollinated species and genera is most likely very recent. Floral modifications for bird pollination which include a long wide periath tube, red to orange coloration and anthers held above the tepals, represent the highest degree of specialization in Iridaceae. They have evolved independently in several lines: within *Watsonia;* in *Antholyza*, an offshoot of *Babiana:* in *Chasmanthe*, related to the *Tritonia-Crocosmia* alliance; in

Anapalina, related to *Tritoniopsis;* and in *Anomalesia* and *Homoglossum*, both allied to *Gladiolus*. All are southern African and largely restricted to the south-western and southern Cape.

The geography of the Iridaceae in the Cape Region is complex. The pattern most often observed in Cape taxa is for a species concentration peak in the Caledon district with decreasing representation north and east. This is true only for a few of several genera of Iridaceae for which there are detailed treatments. *Ixia* (Lewis, 1962) and *Tritonia* conform to this pattern, but in *Moraea* (Goldblatt, 1976) the peak is shifted northwards into the Worcester-Tulbagh District, and in *Homeria* (Goldblatt, in press) the highest number of species occurs in the Cold Bokkeveld-Cedarberg Mountain belt. *Babiana* (Lewis, 1959) and *Lapeirousia* are centred along the west coast and species concentration falls rapidly east of the Caledon District.

A pattern therefore emerges of the concentration of species in the more specialized genera, being shifted to the west, along the coast and in the mountains running north-south, parallel to the coast. This area has a more extreme climate than the southern coast and southern mountains, with reduced rainfall and typically very little or no summer precipitation. The vegetation is shorter and more open, and it seems that this has allowed far greater radiation than along the moister, more heavily vegetated southern parts of the Cape Floristic Region.

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The historical phytogeography of the Disinae (Orchidaceae)

H. P. LINDER*

ABSTRACT

The Disinae (Orchidaceae) are widespread in tropical montane Africa and the Cape temperate region, therefore showing a distribution range typical of a temperate herb in Africa. Centres of endemism and high species richness are recognized in the southern and western Cape Province, the Natal-Transvaal escarpment mountains, the watershed between the Rivers Zaire and Zambesi and the southern highlands of Tanzania, the East African highlands and Madagascar. The number of species and their degree of endemism decrease from south to north. Several regions, e.g. Zimbabwe and West Africa, are outliers of other regions, or overlap zones between regions.

An attempt is made to determine the history of the group by vicariance biogeographical analysis, but the resultant area cladogram is uninformative. This may be due to the vagility of the taxa.

Areas of endemism of supra-specific taxa are determined. These areas appear on recent palaeoenvironmental data to be possible refugia (Cape fold mountains, the South African Drakensberg and the East African Rift Valley mountains), from where the taxa spread when the climate ameliorated after the last glacial. This model is corroborated by recent studies on Cupressaceae, Pooidae and Compositae.

RÉSUMÉ

LA PHYTOGÉOGRAPHIE HISTORIQUE DES DISINÉES (ORCHIDACEAE)

Les Disinées (Orchidaceae) sont largement répandues en Afrique tropicale montagnarde et dans la région tempérée du Cap, montrant donc une aire de distribution typique d'une herbe tempérée d'Afrique. Des centres d'endémisme et une richesse élevée en espèces sont reconnus dans la Province du Cap australe et occidentale, les montagnes de l'escarpement Natal-Transvaal, la ligne de crête entre le Zaïre et le Zambèze, ainsi que les hauts plateaux méridionaux de Tanzanie, les hauts plateaux de l'Est Africain et Madagascar. Le nombre des espèces et leur degré d'endémisme décroît du Sud au Nord. Plusieurs régions, comme le Zimbabwe et l'Afrique de l'Ouest, sont des massifs détachés d'autres régions ou des zones de chevauchement entre régions.

Une tentative est faite pour déterminer l'histoire du groupe par une analyse bio-géographique de la vicariance, mais le cladogramme qui en résulte ne fournit pas d'information. Ceci peut être dû à la mobilité des taxa.

Des régions d'endémisme de taxa supra-spécifiques sont déterminées. Ces régions, suivant des données paléontologiques récentes, semblent être des refuges possibles (les montagnes plissées du Cap, le Drakensberg sud-africain et les montagnes du Graben de l'Est africain), d'où les taxa se sont disséminés quand le climat s'est amélioré après le dernier épisode glaciaire. Cette interprétation est corroborée par de récentes études sur les cupressacées, les pooïdées et le composées.

INTRODUCTION

Over the last 80 years, certain patterns in the distribution of species of the Cape flora and the Afro-montane flora have been documented (Weimarck, 1933, 1936, 1940, 1941; Levyns, 1952, 1955; Wild, 1968, 1975, 1964; Hilliard, 1978; Morton, 1972; Ayodele Cole, 1974; Chapman & White, 1970; White, 1978; Nordenstam, 1969). These have resulted in the recognition of a very distinct Cape flora (Good, 1953; Takhtajan, 1969), whereas the Afro-montane flora has only recently been distinguished as occupying numerous small areas in tropical Africa (White, 1978).

How did the distribution patterns of the species constituting the Afro-montane and Cape floras develop, and what controls them? The answer to this problem can only be found in the evolutionary and phytogeographical histories of the taxa constituting these floras. However, very few taxa have been studied to elucidate their histories (Kerfoot, 1975). The Disinae (Orchidaceae) form an excellent group to study as an example. The subtribe has recently been revised (Linder, 1981a, b, c, d, e, f). It is ubiquitous in the Afro-montane and Cape regions (Fig. 1), and the distribution and biology of the species is relatively well known.

BIOLOGY OF THE DISINAE

The biology of the taxa has to be taken into account, as it may strongly influence the present distribution, the rates of migration, under what conditions speciation may be expected, and how the species would respond to changing environments.

The Disinae are low terrestrial herbs that cannot successfully compete with tall perennial vegetation. Consequently, the majority of the species are restricted to Cape fynbos, Afro-montane grassland or edaphic grasslands, all pyrophytic vegetation types (Knapp, 1973; Vesey-Fitzgerald, 1963; Chapman & White, 1970; Kruger, 1979; Killick, 1978; White, 1978). The distribution is almost limited to temperate climates: a mediterranean climate in the southern and south-western Cape Province (Weather Bureau, 1972) and a cool summer-rainfall climate in the Afro-montane region (Chapman & White, 1970; Ayodele Cole, 1974; Jackson, 1961). Generally, the rainfall regime is between 700 and 2 000 mm p.a. The seeds are very easily dispersed. Each flower produces in excess of 8 000 minute dust-like seeds that are readily dispersed by wind.

Speciation in the Disinae does not appear to be predominantly allopatric, as has been suggested for some other taxa in the Cape flora (Levyns, 1955; Rourke, 1972; Bremer, 1976; Strid, 1972; Goldblatt, 1978, 1981). Although there is some evidence for allopatric speciation, the majority of species in

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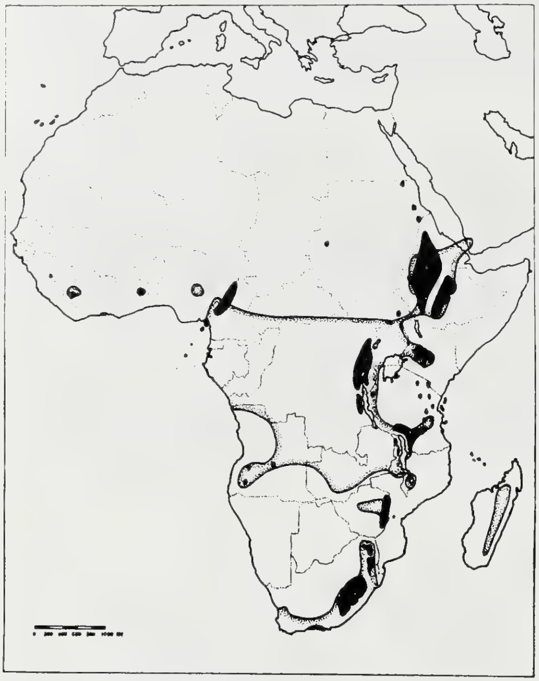

FIG. 1.—Total distribution of the Disinae (outline) in relation to the Afro-montane regions (according to White, 1978) indicated in black.

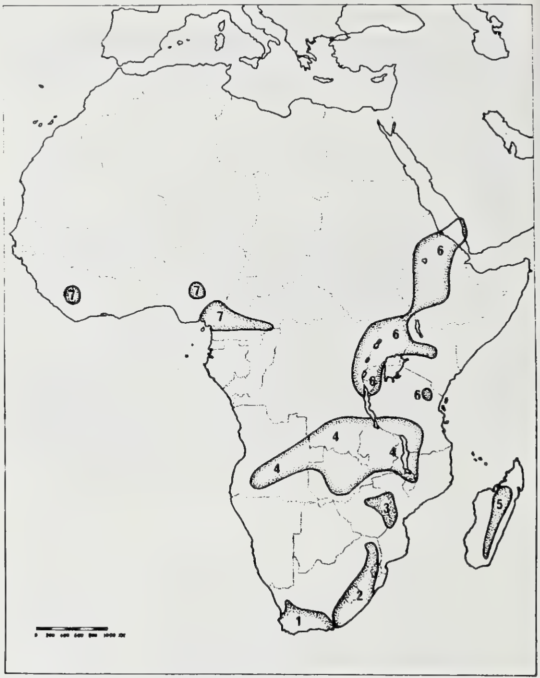

FIG. 2.—Distribution of centres recognized in Africa: 1, Cape centre; 2, Natal-Transvaal centre; 3, Zimbabwe overlap region; 4, South-Central African centre; 5, Madagascan centre; 6, East African centre; 7, West African outlier. The Reunion centre is not indicated.

species groups are more readily analysed along ecological gradients, suggesting that differential selection may be more important than isolation. Various ecological factors appear to be of importance: moisture gradients, altitudinal gradients, substrate types, climate, fog-regimes, annual rainfall, etc.

DISTRIBUTION PATTERNS

To analyse the distribution patterns, 11 more or less geographically isolated areas were delimited. Centres of endemism, overlap regions and outliers were synthesized out of these 11 areas by comparing the species lists of the areas. Centres are defined as having more than 30% endemism, outliers are areas with less than 30% endemism, and with the majority of the non-endemic species held in common with a nearby centre, whereas in overlap regions endemism is less than 30%, and the non-endemic species are held in common with two other centres. The centres recognized are shown in Fig. 2, and the patterns of species richness and supraspecific richness for the centres, as well as the similarities among the centres, is shown in Table 1.

The patterns of decreasing species richness, supra-specific richness and endemism as one proceeds from the Cape northwards are relatively well documented (Baker & Oliver, 1967; Beard, 1963; Rourke, 1980; Weimarck, 1940, 1934; Goldblatt, 1977, 1978; Brenan, 1978). The high degree of endemism in the Cape is also quite typical (Taylor, 1980; Goldblatt, 1978).

TABLE 1.—Species richness, supraspecific richness, levels of endemism and patterns of affinities among the centres

	Cape	Natal-Transvaal	Zimbabwe	South-Central Africa	East Africa	West Africa	Madagascar	Reunion
Cape	99	11	3	0	0	0	1	0
Natal-Transvaal		52	15	9	3	3	3	0
Zimbabwe			23	15	4	5	2	0
South-Central Africa				39	9	7	2	0
East Africa					12	6	1	0
West Africa						8	0	0
Madagascar							7	0
Reunion								1
Number of endemics	89	29	1	17	4	1	3	1
% endemics	90	56	4	45	31	13	43	100
Number of sections	11	10	7	7	4	3	3	1
Number of subgenera	5	5	4	4	3	3	3	1
Number of genera	4	4	4	3	2	2	3	1

Within the Cape Centre, Weimarck (1941) recognized several centres. However, only two centres can be recognized in the Disinae: a western centre and a southern centre with an overlap region on the Cape Peninsula and in the mountains of the Caledon Division. A similar pattern has been recognized for *Leucodendron* (Proteaceae) (Williams, 1972). Typical Cape flora species that extend outside the Cape Floral Region (Goldblatt, 1978) are restricted to Table Mountain Sandstone in the Transkei and southern Natal.

The lack of endemism in Zimbabwe is rather peculiar, as the area is geographically isolated. Wild (1964) recorded a relatively high percentage of endemism for the Chimanimani mountains, and Goldblatt (1977) regarded it as a centre for *Moraea* (Iridaceae). On the whole, the data for Zimbabwe are confusing. As about half of the non-endemic species in Zimbabwe also occur in South Africa, and the other half in South-Central Africa, Zimbabwe is regarded as an overlap region.

The Eastern Cape Province in South Africa totally lacks endemic species. It appears as if this lack of endemism might be common in the Cape floral element in the area.

South-Central Africa is remarkably rich (see also Goldblatt, 1977). The majority of the endemic taxa are quite widespread, reaching from Angola to the Southern Highlands of Tanzania. Six taxa are restricted to the high mountains around the northern edge of Lake Malawi. The area is generally rich in endemic species (Hedberg *et al.*, 1980) and has a remarkably rich orchid flora (Williamson, 1979).

Although several studies have indicated that the montane grassland of the West African mountains is most closely related to that of the East African highlands (Morton, 1972; Hamilton, 1974; Ayodele Cole, 1974; Hall & Medler, 1975), the Disinae are, with one exception, common to the South-Central African centre. The area is therefore regarded as an outlier of the South-Central African centre. Species richness decreases rather rapidly from east to west in West Africa.

The East African centre has four (31%) endemic species. There is an interesting distribution pattern, connecting the Kenyan uplands to the Ethiopian highlands via Mt Elgon, Mt Kadam, Mt Moroto and the Imatong mountains.

Wild (1975) showed that Madagascar shared many more species with southern Africa than with eastern Africa, a pattern which is corroborated by the distributional data of the Disinae. There is a single endemic species on Reunion. Levyns (1937) recorded a similar situation for the Composite genus *Stoebe*.

Clearly, the phytogeographical patterns in the Disinae agree in the main with the general patterns found in the Cape and Afro-montane floras.

BIOLOGY AND ENVIRONMENT AS A PREDICTOR OF DISTRIBUTION

The hypothesis that the distribution patterns in the Disinae are correlated to, and probably caused by, the combination of the biology of the species and the present environment predicts some of the observed patterns, but not others. The total distribution range in Subsaharan Africa is clearly related to the present environment. The intervals in Africa are also related to the environment: a change in substrate in the Cape-Natal interval, change in the monthly distribution of precipitation in the Western-Southern Cape interval, and regions of inhospitable vegetation in most of the tropical intervals. However, this hypothesis cannot account for the absence of the subtribe from the Mediterranean basin, where the habitat appears to be eminently suitable, or for the patterns of diversity and endemism observed among the various centres.

Consequently, it is necessary to investigate the history of the subtribe (i.e. migrations and past distributions determined by palaeoclimates) to provide an alternative hypothesis on the evolution and diversification of the subtribe.

HISTORY

The most rigorous method for reconstructing the history of a group in the absence of fossil evidence is by vicariance biogeography (Platnick & Nelson, 1978; Rosen, 1978; Humphries, 1981). In this method, the phylogenetic classification of the group is superposed over the geographical regions, to form an area cladogram (Fig. 4). This is based on the cladogram in Fig. 3. (from Linder, 1982). The area cladogram is clearly uninformative as to history of the group. This could be due to the invalidity of the assumption in vicariance biogeographical analyses of the absence of long-distance dispersal.

A less rigorous approach is to analyse the distributions of supra-specific taxa, and to study the occurrence of patterns of vicariant taxa. Supra-specific groups, especially at sectional level, show striking patterns: (a) Only one section contains species in the Cape Centre as well as the tropical centres, and in this section the Cape species belong to different series from the tropical species; (b) With one exception, all the sections found in tropical

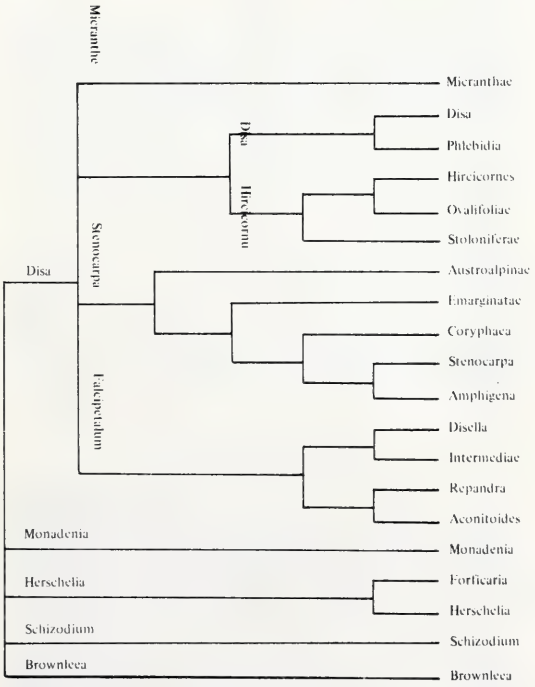

FIG. 3.—Cladogram of the Disinae, according to Linder (1982).

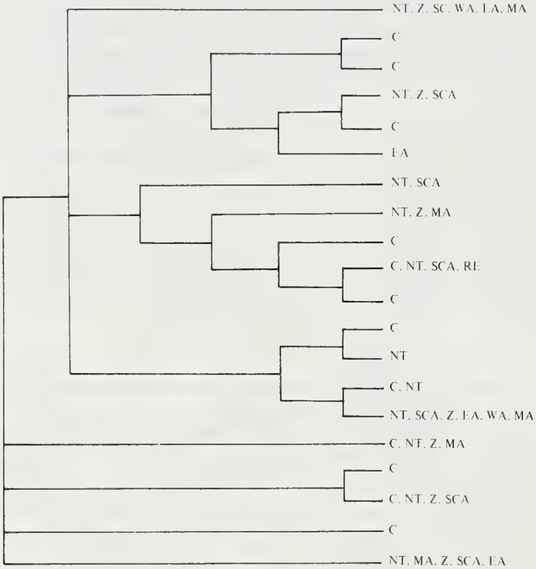

FIG. 4.—Area cladogram of the Disinae, based on Fig. 3. C = Cape centre; NT = Natal-Transvaal centre; SCA = South-Central African centre; EA = East African centre; WA = West African outlier; MA = Madagascar; RE = Reunion.

Africa are represented in the Natal-Transvaal centre. However, in some of the sections there is differentiation at the series level between the Natal-Transvaal centre and the South-Central African Centre; (c) There is one section endemic to the high mountains along the western Rift Valley; (d) There are no sections or series endemic to Madagascar or to West Africa.

Specific vicariance provides some interesting information. *Disa borbonica,* the only species on Reunion, is closely related to *D. vaginata* from the Western Cape, while the only endemic species on Madagascar, *Disa incarnata,* is very near to *D. scutellifera* from East Africa. Within the Cape Centre, there are nine cases of species replacement from the Western Cape to the Southern Cape.

These data indicate three 'source' regions for the Disinae in Africa (the Cape fold mountains, the Natal-Transvaal escarpment and the Rift Valley mountains) from where the taxa spread to occupy their present range. Possibly the watershed between the Zaire and Zambezi may also have to be included. Maybe these 'source' regions are refugia.

PALAEOENVIRONMENTS

The data on climatic fluctuations (and by inference environmental changes) in the last 25 000 years in Africa are patchy. Hamilton (1974, 1976), Livingstone (1975) and Nicholson & Flohn (1980) have reviewed the available data for East and North-central Africa. They suggest that the climate was cold and dry from 10 000 to 25 000 years ago, resulting in the replacement of Afro-montane vegetation (the habitat of the Disinae) by dry savanna grassland. Between 10 000 and 1 000 years ago the present Afro-montane regions were occupied by Afro-montane forest, possibly with patches of Afro-montane grassland. The present large expanses of Afro-montane grassland possibly only date from the advent of iron-smelting, leading to the rapid decimation of the forests (Chapman & White, 1970; Hall & Medler, 1975; Hall 1971). This could mean that the mountains of West Africa did not have suitable habitats for Disinae until either 10 000 years B.P. or 1 000 years B.P., whereas the higher and more extensive mountains of East Africa are more likely to have maintained at least some suitable habitats. The data for South-Central Africa are lacking. Scott in this symposium showed that for the Transvaal between 30 000 and 10 000 years B.P. sclerophyllous vegetation, possibly Drakensberg macchia, was more widespread. This could mean that the habitat for the Disinae was more widespread during this period, as several species are at present associated with macchia. For the Cape Region, Martin (1968) and Schalke (1973) suggested that prior to 30 000 years B.P. the Knysna forests were widespread. Evidence from archaeological work indicates that during the last glacial (10 000 to 25 000 years ago) conditions were colder and drier, leading to the replacement of the forests by grasslands (Klein, 1972; Parkington, 1978), which were replaced by scrubby vegetation after the glacial. It appears unlikely that these fluctuations could have led to the loss of the characteristic Cape flora from the Cape fold mountains, or to the disappearance of the Afro-montane vegetation from the Drakensberg, whereas this could well have been the case on the lower mountains, such as the mountains of the Eastern Cape Province.

These data and interpretations corroborate the historical scenario suggested in the previous section, as it appears to be unlikely that the Disinae lost their habitats in the Cape fold mountains and the South African Drakensberg during the Pleistocene, whereas most of the available, if not all, habitat was lost in West Africa and East Africa, probably with the exception of the high Rift Valley mountains.

CONCLUSIONS

The overall distribution of the Disinae in Africa is determined by their biology. On this basis, they may be described as a temperate African element.

It is not possible to determine where the Disinae originated. This appears to have been obscured by the vagility of the taxa. However, three, and possibly four, refugia can be determined. These are the Cape fold mountains, the South African Drakensberg and the East African Rift Valley mountains, with a fourth possible refugium on the watershed between the Rivers Zaire and Zambezi. These areas are characterized by high levels of endemism at the specific level, and endemism at the sectional level. Present palaeoenvironmental interpretations indicate that it is unlikely that the temperate habitat was entirely lost from these regions during the last glacial, while the less mountainous areas appear to have been quite arid. When the climate ameliorated about 10 000 years ago, these refugia acted as source areas, from where the Disinae spread into West Africa, Zimbabwe, Madagascar, Reunion and possibly South-Central Africa (Fig. 5).

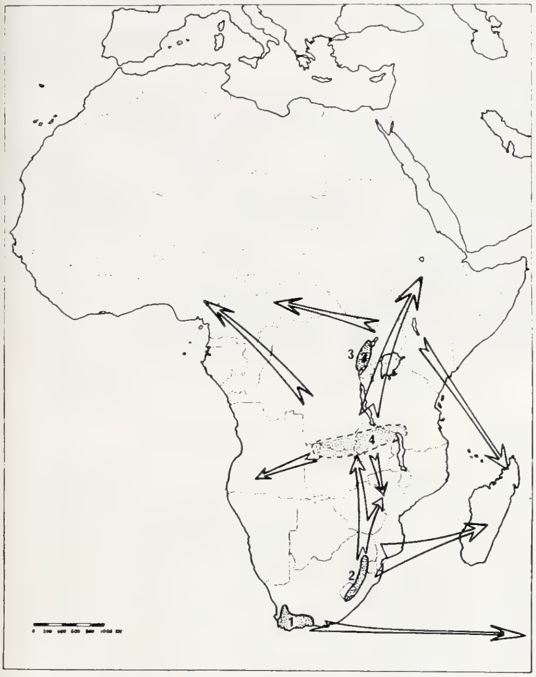

FIG. 5.—Suggested Pleistocene 'refugia': 1 = Cape fold mountains; 2 = South African Drakensberg; 3 = East African Rift mountains; 4 = possible refugium on the watershed between the rivers Zaire and Zambesi. The arrows indicate the probable directions of post-glacial migration.

This may well be a general pattern for African temperate plants, and analyses done on the Pooidae (Clayton, 1976), the Compositae of Natal (South Africa) (Hilliard, 1978) and the Cupressaceae (Kerfoot, 1975) corroborate this hypothesis.

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Ethiopian flora project

O. HEDBERG*

ABSTRACT

After thorough planning, an Ethiopian Flora Project has recently been initiated, financed by the Ethiopian Science and Technology Commission from a Swedish grant. The planning was effected by a working group including representatives of the Biology Department at Addis Ababa University and the Institute of Systematic Botany in Uppsala as well as some international experts selected by AETFAT, and was finalized by an Ethiopian Flora Committee. The project leader is Professor Tewolde Berhan G. Egziabher in Addis Ababa, assisted by an Ethiopian secretariat under the Director of the National Herbarium. A European counterpart secretariat, headed by the author, has also been organized with Dr I. Hedberg as co-ordinator. Collecting expeditions to insufficiently known areas, loans from the Addis Ababa Herbarium to collaborating taxonomists, and other activities inside Ethiopia are organized by the Ethiopian secretariat, whereas the Uppsala secretariat is responsible for the initiation and co-ordination of the taxonomic revisions and family accounts needed for the Flora. Collaborators for several of the roughly 200 families of Ethiopian vascular plants have already been secured, but many more remain to be covered. AETFAT members with specialist knowledge of the remaining families are requested to help fill the gaps in our list of contributors.

RÉSUMÉ

PROJET DE FLORE ÉTHIOPIENNE

Après une planification minutieuse, un Projet de la Flore éthiopienne a récemment vu le jour, financé par la Commission Éthiopienne des Sciences et de la Technologie, à partir d'une subvention suédoise. La planification a été effectuée par un groupe de travail qui incluait des représentants du Département de Biologie à l'Université d'Addis Ababa et de l'Institut de Botanique Systématique d'Uppsala ainsi que certains experts internationaux choisis par AETFAT, et elle fut mise au point par un Comité de la Flore Éthiopienne. Le chef du projet est le Professeur Tewolde Berhan G. Egziabher d'Addis Ababa, assisté par un secrétariat éthiopien sous l'autorité du Directeur de l'Herbarium National. Un secrétariat européen correspondant, sous la direction de l'auteur, a également été organisé avec le Dr. I. Hedberg comme coordinateur. Les expéditions de récolte dans les régions insuffisamment connues, les prêts faits par l'Herbarium d'Addis Ababa aux taxonomistes qui collaborent et d'autres activités en Ethiopie sont organisés par le secrétariat éthiopien, tandis que le secrétariat d'Uppsala est responsable de la mise en route et de la coordination des révisions taxonomiques et des traitements des familles nécessités pour la Flore. Des collaborateurs pour plusieurs des quelque 200 familles de plantes vasculaires éthiopiennes ont déja été assurés, mais beaucoup d'autres doivent encore être couvertes. Les membres AETFAT ayant une connaissance spécialisée des familles restantes sont requis d'apporter leur aide pour combler les lacunes dans notre liste de collaborateurs.

INTRODUCTION

The botanical exploration of the inland regions of tropical Africa started rather late (see accounts in Fernandes, 1962), but today most of the continent is considered to be comparatively well explored (Hepper, 1979). One of the earliest countries in Africa to yield botanical material was Ethiopia, but difficulties of access and travel made its exploration rather patchy and even today most of this country is poorly known botanically (Moggi, 1976).

The first general flora of Tropical Africa was the classical 'Flora of Tropical Africa' (Oliver, 1868–Hill, 1937). This was a very ambitious project, but its scope was too wide to make it really useful for any of the individual countries it comprised. When publication was discontinued, it was not quite complete and the earlier parts were already long out of date. Even before World War II the need for regional or national floras was becoming more and more obvious, and flora projects were started for a number of regions and countries, such as Flora of West Tropical Africa (Hutchinson & Dalziel, 1927–1936 — a second revision edited by Keay and Hepper appeared 1958–1972), Conspectus Florae Angolensis (Exell & Mendonça, 1937–), Flore du Congo et du Ruanda Burundi (1948–), Flora of Tropical East Africa (Turrill & Milne Redhead, 1952–), Flora Zambesiaca (Exell & Wild, 1960–), Flore du Cameroun (Letouzey, 1963–) and others. The practical and economic importance of a flora for a developing country was well understood by the colonial powers (cf. Brenan, 1963), and they were quite willing to supply the money and manpower needed to prepare such floras for their colonies. Decolonization in the middle of this century obviously caused administrative and economic difficulties for these projects, but fortunately the earlier colonial powers in most cases took responsibility for the continuation of the flora projects they had started.

The only tropical African country which, apart from a brief Italian occupation, remained independent during the colonial epoch was Ethiopia, for which consequently no flora project was initiated by a colonial power. The explorations and revisional work started during the Italian occupation led to the foundation of a colonial herbarium in Florence and the starting of the series 'Adumbratio Florae Aethiopicae' (Chiarugi, 1953).

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EARLIER FLORA WORK

The absence of current political incentives to produce an Ethiopian Flora does not mean that the country has been neglected by botanists in the past. On the contrary, it was one of the first African countries to have its flora enumerated in a published work, namely A. Richard's 'Tentamen Florae Abyssinicae' (1847–1851). The primary object of this book was to document the botanical findings of the two young French naturalists, Antoine Petit and Quartin Dillon, both of whom died in unfortunate circumstances in Africa, but it also enumerates the earlier series of invaluable material collected by Schimper. It therefore constitutes a very useful conspectus of what was known of the Ethiopian flora at that time, and contains original descriptions of hundreds of African plant species. Numerous smaller contributions have subsequently been published on various Ethiopian plants, as well as checklists for a number of areas, but no recent comprehensive account of the flora has appeared. As a preparation for a new Flora of Ethiopia, Cufodontis (1953–1972) published an annotated compilatory checklist, 'Enumeratio Plantarum Aethiopicae' — but this, of course, had neither keys nor descriptions. How far from complete it is, may be indicated by the fact that the account of the family Leguminosae prepared for the new flora project contains about 100 species not enumerated by Cufodontis, many of them new. The need for an up to date flora of the country has been increasingly felt, both inside Ethiopia and among botanists working on other parts of tropical Africa.

NATIONAL AND INTERNATIONAL IMPORTANCE OF AN ETHIOPIAN FLORA

On the international scene, a Flora of Ethiopia is badly needed, because so many East African plants were described from Ethiopian material. As long as the variation of the Ethiopian type population is unknown, the taxonomy of such a group is often difficult to unravel. Since Ethiopia is one of Vavilov's centra of origin of cultivated plants, the Ethiopian flora is of large practical importance for plant breeding. It is evidently the country of origin for cultivated coffee, *Coffea arabica* (Friis, 1979) as well as for ensete (Smeds, 1955) and tef *(Eragrostis abyssinica).* It also houses a rich store of genetic variability of, *inter alia,* barley *(Hordeum)* and wheat *(Triticum),* and it is therefore not surprising that a gene bank has been started in Addis Ababa.

This brings us to the national importance of an Ethiopian flora (cf. also Brenan, 1963). Access to such a flora and to a National Herbarium will make possible, rapid and accurate naming of plant specimens. This again will very much facilitate vegetation classification and land use planning, leading to long needed improvements in agriculture, forestry and conservation of nature. A new flora is also very much in demand for scientific research and teaching, at the University as well as at secondary schools. When I visited Ethiopia in the autumn of 1967, I was informed about this need by representatives of several government departments and asked to help in soliciting support for an Ethiopian flora — which led me to investigate the possibilities for such a project.

HISTORY OF THE FLORA PROJECT

After preliminary discussions in the late sixties involving Prof. R.E.G. Pichi Sermolli, Prof. H.C.D. de Wit and others, a small meeting was convened at the 7th Plenary Meeting of AETFAT in Munich to discuss the planning of a Flora of Ethiopia. A planning committee and an advisory committee for the Flora Project were elected. After a considerable amount of discussion, both during occasional meetings and by correspondence, the planning committee produced a plan for a Flora of Ethiopia, which was presented at the 8th Plenary meeting of AETFAT in Geneva in 1974. As chairman of the planning committee, I had been asked to try to find ways of funding the project. It soon turned out, however, that neither the committee nor any of the European botanical institutions involved stood a good chance to raise the money required. The Ethiopian participation in the planning, which had been rather weak from the start, gradually became more powerful, and some time after the revolution an Ethiopian Flora planning committee was founded. At the 9th Plenary Meeting of AETFAT in Las Palmas in 1978 it was therefore decided to dissolve the advisory and planning committees of AETFAT and leave the initiative required to the Ethiopian Flora planning committee. This committee later applied for funding of the project from the grant given by SAREC (Swedish Agency for Research Co-operation with Developing Countries) to Ethiopia and distributed by the Ethiopian Sciences and Technology Commission. The Commission put a high priority on the flora project, and from 1st July 1980 the project has been under way. Funds have been granted for an initial 2½ year period, and it is hoped that SAREC together with the University of Addis Ababa will provide the additional funds needed for completion of the project, estimated to take a period of 10–15 years.

PURPOSE AND ORGANIZATION

The purpose of the Ethiopian Flora Project is threefold: (1) to write up an Ethiopian Flora within the shortest possible time, (2) to strengthen the Ethiopian National Herbarium in Addis Ababa with its library, and (3) to train Ethiopian taxonomic botanists.

The project leader is Professor Tewolde Berhan Gebre Egziabher at the Biology Department in Addis Ababa, who has at his disposal a secretariat under the Director of the National Herbarium. A European counterpart secretariat has been organized at my Institute in Uppsala with Dr Inga Hedberg as co-ordinator. The latter secretariat is responsible for the initiation and co-ordination of the taxonomic revisions and family accounts needed for the Flora. It also assists in the purchase of equipment and literature needed for the project and effects payments outside the Ethiopian border. The field trips and collecting needed in Ethiopia as well as loans from the National Herbarium to collaborating botanists are organized by the secretariat in Addis Ababa, whereas the postgraduate training of Ethiopian taxonomic botanists required for the project is organized in collaboration between Addis Ababa and Uppsala.

The Flora is planned to appear in eight small volumes, seven of which will include the taxonomic accounts and follow the family sequence used in J. Hutchinson, Families of Flowering Plants Edn 1 (1926–1934). These volumes will appear as soon as they are completed, starting with Volume 3 (Grossulariaceae–Umbelliferae). A sample treatment has been prepared and distributed to all registered contributors.

For the 200-odd family revisions required for the Flora we are hoping for assistance from the many taxonomic specialists available, some of whom have already contributed to other national or regional African floras, and most of whom are no doubt members of AETFAT. Practically all AETFAT members should already have received a first circular soliciting collaboration, also reproduced in AETFAT Bull. 30, and a considerable number have pledged support for our project. In this way we have catered for practically all the families of the first volume to be published (Vol. 3), and a considerable proportion of the later ones. But many more families need 'revisers' and I therefore appeal to you all to help fill the gaps remaining in our list of collaborators. A pamphlet listing the families remaining to be tackled is available.

In spite of the collaboration already pledged and that expected in future, there will obviously always remain a number of groups for which no external collaborator can be found, but which must be tackled by a taxonomist employed by the project. The necessity of having all family accounts for a certain volume ready before publication may also call for urgent action by project staff. Since some of our external collaborators may find it difficult or impossible to visit (or borrow from) all the important herbaria housing Ethiopian and East African collections, it may be necessary to provide them with some service at those herbaria. For these reasons, the Planning Committee has engaged the services of one fulltime botanical taxonomist, Dr Kaj Vollesen, to be based primarily at Kew. In 1982 we are hoping to employ a second botanist for the same purpose. We shall also endeavour to select Ph.D. thesis projects for Ethiopian and Swedish students working on the African flora, so as to benefit the project as much as possible.

PROGRESS ACHIEVED

The most conspicuous progress achieved so far for the project is that the family Leguminosae has been completed and is ready for printing — it is hoped to distribute this as a preprint for the flora. Economically, Leguminosae is one of the two most important families in Ethiopia and comprises roughly 10% of the flowering plants of the country. The revision of the sub-family Papilionoideae was completed by Dr Mats Thulin (supported by a grant from the Swedish Natural Science Research Council), that of Mimosoideae by Mr Asfaw Hunde (sponsored by the Salen Foundation and the Swedish Institute), and the revision of the Caesalpinioideae was contributed by Dr Roger Polhill, Kew. Draft manuscripts of some further families of Volume 3 of the Flora have been received, and it is hoped to have the whole of this volume ready for publication within two years.

As regards the National Herbarium in Addis Ababa, considerable progress has been made. The herbarium has been moved from its earlier situation to much more spacious premises, made vacant through the moving of the Biology Department into a new building. New herbarium cupboards are being installed, new equipment has been bought, the staff increased, and this progress will continue during the coming years.

As regards post-graduate training, one M.Sc. student specializing in palynology, spent five months in Uppsala and Stockholm obtaining good grounding for his work. The curator of the National Herbarium in Addis Ababa, Mesfin Tadesse, spent nine months in Uppsala following a postgraduate course and started work on the genera *Bidens* and *Coreopsis* in Ethiopia for a Ph.D. thesis. Another Ph.D. student, Sebsebe Demissew, is scheduled to spend most of the academic year 1981/82 in Uppsala for a similar purpose.

CONCLUSION

In conclusion, I would like to suggest that the Ethiopian Flora Project described above, be regarded as a child of AETFAT. It was conceived through collaboration between botanists from three different European herbaria, whose contacts had been built up within AETFAT. The fundamental planning was achieved by a committee nominated at an AETFAT meeting, and the completion cannot be accomplished without substantial international collaboration in the best AETFAT spirit. I would therefore like to conclude my paper by requesting members of AETFAT to assist in taking good care of this child of ours!

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The distribution of *Monechma* (Acanthaceae) species in southern Africa

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ABSTRACT

The distribution of 19 species of *Monechma* in southern Africa is given and the manner in which their occurrence is related to rainfall is discussed. The possibility of a centre of speciation lying in south-west Namibia/South West Africa is considered.

RÉSUMÉ

LA RÉPARTITION DES ESPÈCES MONECHMA *(ACANTHACEAE) EN AFRIQUE AUSTRALE*

La répartition des 19 espèces de Monechma *en Afrique australe est donnée et la manière dont leur présence est liée aux précipitations est discutée. La possibilité d'un centre de spéciation dans le Sud-Ouest de la Namibie/Sud-Ouest Africain est considérée.*

INTRODUCTION

The genus *Monechma* Hochst., closely related to *Justicia* L., is an African genus of about 60 species. These species occur in both tropical and sub-tropical regions and one extends as far as India. The genus is represented in southern Africa, i.e. the area covered by the Flora of Southern Africa, which includes South Africa, Botswana and Namibia, by 19 species. Except for one, *M. leucoderme* (Schinz) C.B.Cl., which is regularly found on granite, the local *Monechma* species all show a preference for lime and are most commonly found on substrates containing it. On the whole, *Monechma* plants are well-adapted to survival in a harsh environment, being finely attuned to xerophytic conditions and are tough, hardy plants which occupy a wide variety of habitats in generally arid areas. A rainfall map of southern Africa is provided in Fig. 1.

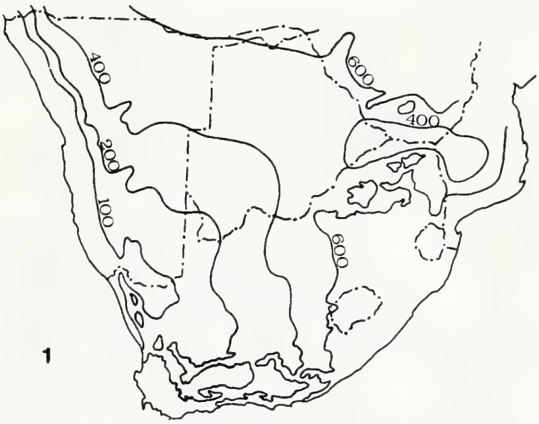

FIG. 1.—Rainfall map of southern Africa based on Jackson's Climatological Atlas of Africa.

DISTRIBUTION OF SPECIES

The species may, for convenience, be roughly divided into three groups based on the size of the area which each species occupies. The divisions are quite arbitrary and the distributional areas are only large or small in relation to one other.

1. The two largest species, *Monechma debile* (Forsk.) Nees and *M. divaricatum* (Nees) C.B.Cl., are not endemic in southern Africa. *Monechma debile* is the most widespread species in the entire genus and the only one also having extra-African distribution, occurring as far afield as India. It often appears as a weed or a ruderal and is one of only two annual species in southern Africa. Apart from the extreme north of the Transvaal where the rainfall is between 200–400 mm per annum, *M. debile* is not generally found in areas where the rainfall is less than 400 mm per annum and in this respect it differs markedly from most of the other species. (Fig. 2 & Table 1).

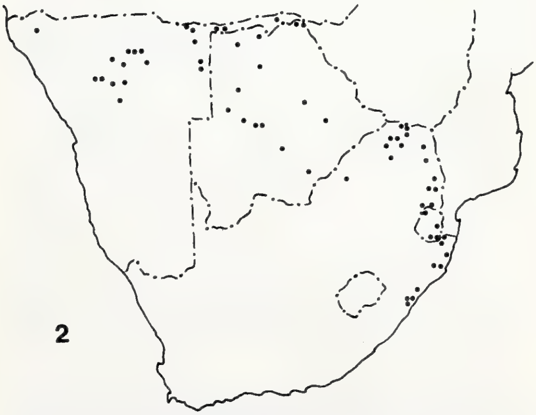

FIG. 2.—Distribution of *Monechma debile.*

The second species with a wide distribution is *M. divaricatum,* which also occurs beyond the borders of southern Africa. It is not as restricted as *M. debile* within our area, appearing quite generally in the northern Cape and throughout Namibia, though not

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TABLE 1.—Analysis of species according to rainfall requirements, measured in mm per annum

Species	Under 100	100 and under 200	200 and under 400	400 and over
crassiusculum	×			
callothamnum	×			
mollissimum	×			
saxatile	×			
salsola	×			
calcaratum	×	×		
leucoderme	×	×		
desertorum	×	×		
distichotrichum	×	×	×	
cleomoides	×	×	×	
spartioides	×	×	×	
incanum	×	×	×	
genistifolium	×	×	×	×
divaricatum		×	×	×
serotinum		×		
robustum		×		
grandiflorum		×		
tonsum		×	×	
debile		×	×	
Totals	13	13	8	3

where the rainfall is less than 100 mm per annum, nor is it found in the southern Transvaal, Orange Free State, Lesotho, most of Natal or the southern and eastern Cape (Fig. 3).

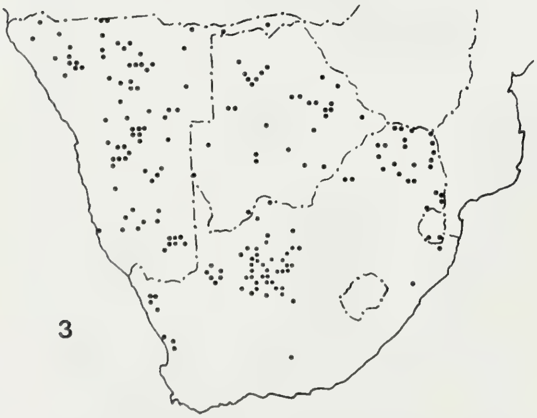

FIG. 3.—Distribution of *Monechma divaricatum.*

2. Seven species, occupying medium-sized distributional areas, are placed in the second group, *viz. M. incanum* (Nees) C.B.Cl., *M. spartioides* (T. Anders.) C.B.Cl., *M. genistifolium* (Engl.) C.B.Cl., *M. cleomoides* (S. Moore) C.B.Cl., *M. distichotrichum* (Lindau) P. G. Meyer, *M. leucoderme* (Schinz) C.B.Cl. and *M. desertorum* (Engl.) C.B.Cl.

Monechma incanum and *M. spartioides* are largely sympatric and, except for isolated instances, neither species occurs where the rainfall exceeds 400 mm per annum. *M. spartioides* is most heavily concentrated in the Orange River basin, from the Vaal-Orange confluence westward towards the coast and into southern Namibia, whereas *M. incanum* is more generally scattered in its distribution throughout the same area (Fig. 4).

M. genistifolium (in which *M. australe* P. G. Meyer is included as a subspecies) extends in a broad band from north-west to south-east Namibia and into the northern Cape as far as Prieska. The two subspecies occupy different parts of the distributional area, subspecies *genistifolium* being confined to the northern half and subspecies *australe* to the

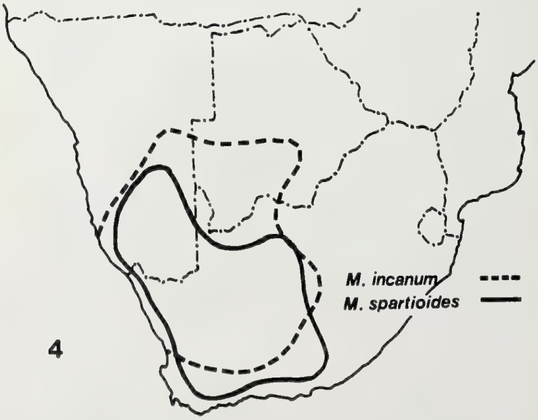

FIG. 4.—Distribution of *Monechma spartioides* and *M. incanum.*

southern. The bulk of this species is found in the 100–200 mm per annum rainfall belt, but the margins are both above and below these levels (Fig. 5). *M. cleomoides* (as defined here it includes *M. arenicola* Engl.) is difficult to assess, being more of a collection of quite different groups of plants connected only loosely by their indumentum, rather than a clearly defined taxonomic entity and any inferences drawn from the distribution of these plants could therefore be misleading. They all, however, occur in a well-defined band from Angola in the north, down the western half of Namibia to Sandverhaar in the south (Fig. 6).

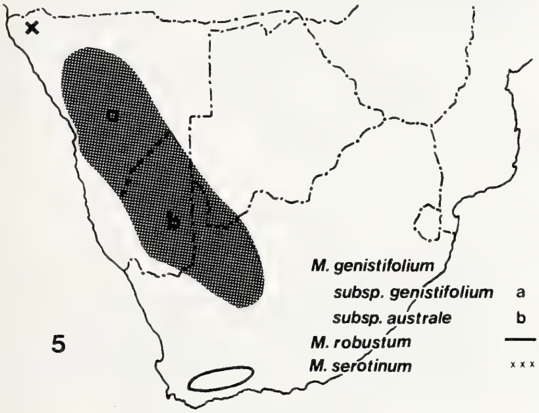

FIG. 5.—Distribution of *Monechma genistifolium* subsp. *genistifolium* and subsp. *australe*, *M. robustum* and *M. serotinum*.

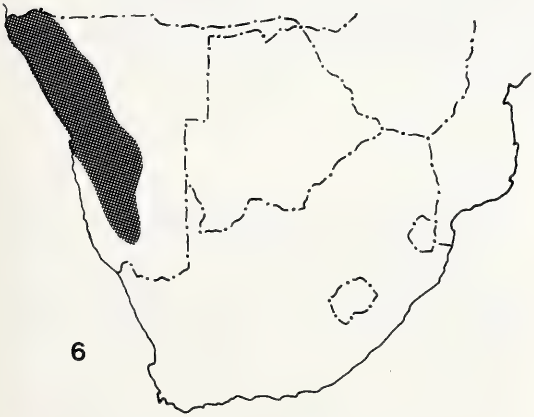

FIG. 6.—Distribution of *Monechma cleomoides*.

The last three species in this group have the most restricted distributions and overlap one other in the south-western corner of Namibia. *M. distichotrichum* extends from Aus in southern Namibia to the Prieska district of the Cape, *M. leucoderme* seems to be confined to mountainous areas and is found from the Orange River northwards as far as Windhoek and *M. desertorum*, as its name implies, occurs mainly in and around the Namib desert from Uis southward to Witpütz and eastwards as far as Holoog. *M. desertorum* is an annual species and occurs only where the rainfall is less than 200 mm per annum, about half of the recorded specimens having been collected in localities where the rainfall is less than 100 mm per annum. On the other hand, both *M. distichotrichum* and *M. leucoderme* have been collected in three different rainfall belts viz. under 100, 100–200 and 200–400 mm per annum. Contrary to published records (Acocks, 1975; Wilman, 1946), *M. desertorum* does not occur anywhere in South Africa, being restricted to Namibia. Plants from the Cape identified as this species are almost certainly examples of *M. distichotrichum* (Fig. 7).

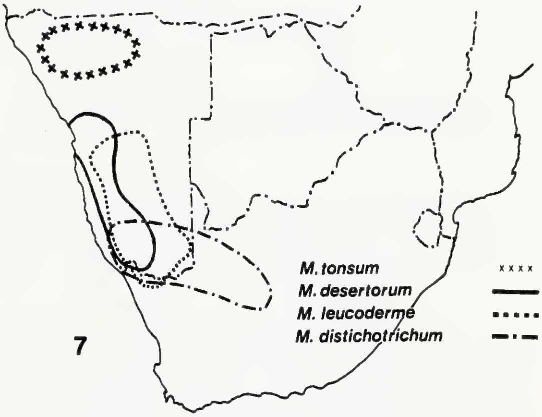

FIG. 7.—Distribution of *Monechma tonsum*, *M. desertorum*, *M. leucoderme* and *M. distichotrichum*.

3. The third group, containing the smallest, most restricted species is probably the most interesting of the three groups as it seems to provide evidence for a centre of speciation, certainly of distribution for the southern African species as a whole. The group comprises 10 species. *M. salsola* (S. Moore) C.B.Cl. is an Angolan species which only just enters the area of the Flora in northern Namibia, where it is found in a few places in Kaokoland. It is also an arid area species, occurring only where the rainfall is less than 100 mm per annum (Fig. 8). Also in the north, between the 100 mm and 200 mm isohyets, is the single locality of *M. serotinum* P. G. Meyer, known only from its type gathering (Fig. 5). Further east, from Ohopoho to the area around Etosha Pan and south to Khorixas (Welwitschia), *M. tonsum* P. G. Meyer is found. The latter does not occur where the rainfall is less than 200 mm per annum, but is also found where precipitation is in excess of 400 mm per annum and may therefore be grouped with the tropical species further north, although its distribution beyond Namibia, if any, is not known (Fig. 7).

With the removal of the three species mentioned above, the remaining taxa may be described as very restricted, endemic, arid-area species. With the exception of *M. robustum* P. Bond, which occurs in the southern Cape, in a small area between Anysberg and Oudtshoorn, all the species occur in the south of Namibia and the Orange River basin (Figs 5 & 8). They are *M. calcaratum* Schinz, *M. callothamnum* J. Munday ms. (Munday, 1980), *M. crassiusculum* P. G. Meyer, *M. grandiflorum* Schinz,

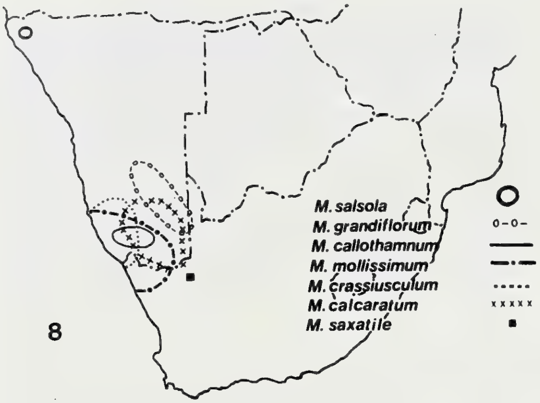

FIG. 8.—Distribution of *Monechma salsola, M. grandiflorum, M. callothamnum, M. mollissimum, M. crassiusculum, M. calcaratum* and *M. saxatile.*

M. mollissimum (Nees) P. G. Meyer and *M. saxatile* J. Munday ms. (Munday, 1980).

DISCUSSION AND CONCLUSION

In a paper on aridity as a stimulus to plant evolution, Stebbins (1952) presents evidence 'in favour of the hypothesis that environments limiting or deficient in one all important factor, moisture, have often promoted rapid evolution.' The southern half of Namibia, particularly the south-western corner, is a very arid region, and is indeed such an environment. The last six species listed in the third group above all occur in areas where the rainfall is less than 200 mm per annum and it is tempting to regard this region as the centre of speciation for the southern African species (Fig. 8).

The position of *M. robustum* is problematical. It is not known whether to regard it as a relic species, perhaps pushed to its present position by *M. incanum* or *M. spartioides* or whether it has recently evolved in its present position.

Some *Monechma* species appear to have very definite rainfall requirements whereas others have a much wider tolerance of varying conditions and their distribution is scattered across several rainfall belts (Table 1). Where a species, as reflected by its collected specimens, shows a certain moisture preference, but has a few anomalous recordings from exceptional localities, it is quite possible that these localities have, in fact, a local microclimate in keeping with the requirements of the species, in spite of their displacement.

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A phytogeographic survey of Southern Benin

G. PARADIS*

ABSTRACT

Southern Benin has a dry subequatorial climate with a rainfall gradient from 850 mm in the west to 1 500 mm in the east, the geomorphology is varied and the vegetation has been subjected to strong human influence. There are numerous plant formations, namely:

1, forest islands which are probably relics of the primitive vegetation and include (a) dense semi-deciduous forests of several types, (b) swamp forests of two types, (c) periodically flooded forest of two types, (d) *Lophira lanceolata* (Hutchinson & Dalziel, 1954–72) woodlands and (e) mangrove swamps;

2, formations which are probably derived and include (a) thickets of several types, (b) tree savannas and shrub savannas, (c) grassy savannas and prairies varying according to soil characteristics and (d) halophytic grasslands; and

3, floating vegetation on fresh-water lakes.

RÉSUMÉ

APERCU PHYTOGEOGRAPHIQUE SUR LE SUD BÉNIN

Le Sud-Bénin, en climat subéquatorial sec avec un gradient de pluies d'ouest en est (de 850 à 1 500 mm), ayant une géomorphologie variée et ayant subi un fort impact anthropique présente de nombreuses formations végétales. On peut distinguer:

1, Des îlots forestiers (restes vraisemblables de la végétation primitive) comprenant des: (a) forêts denses semi-décidues, de plusieurs types et occupant les plateaux, les bords de vallée et la dépression argileuse de la Lama, (b) forêts marécageuses de deux types (un type à nombreuses espèces dans les vallées continuellement inondées et à écoulement permanent de l'eau; un type dominé par Ficus congensis *dans les dépressions littorales à eau stagnante en saison sèche), (c) forêt périodiquement inondée de deux types (un sur sable littoral à* Symphonia globulifera; *un sur les terrasses de bord des fleuves), (d) forêt claire à* Lophira lanceolata *sur le sable roux littoral, (e) mangrove en bordure de la lagune de l'ouest;*

2, Des formations vraisemblablement dérivées,, comprenant: (a) des fourrés (à Manilkara obovata *près de l'océan; à* Dalbergia ecastaphyllum *près des mangroves; à nombreuses espèces près des îlots de forêt dense semi-décidue, (b) des savanes arborées et arbustives (à* Lophira; *à* Mitragyna inermis *et* Phoenix reclinata *dans les vallées; à* Terminalia glaucescens *et autres espèces dans la dépression de la Lama), (c) des savanes herbeuses et des prairies variées suivant les caractères du sol (à* Ctenium newtoni; *à* Andropogon gayanus; *à* Vetiveria nigritana; *à* Cynodon dactylon; *à* Loudetia phragmitoïdes; *à* Echinochloa pyramidalis; *à* Typha australis; *à* Paspalum vaginatum . . .*), (d) des pelouses halophiles à* Sesuvium portulacastrum *et* Philoxerus vermicularis;

3, Une végétation flottante sur les lacs d'eau douce (à Cyclosorus striatus, Pistia stratiotes . . .*).*

L'action humaine actuelle tend à détruire les derniers îlots forestiers et à favoriser les fourrés et la végétation herbeuse.

Since Adjanohoun's report on conservation of vegetation in Le Dahomey (1968), several investigations have been carried out on the vegetation of Southern Benin (see References). This article endeavours to take stock of the phytogeographic knowledge of that region.

1 ENVIRONMENT

1.1 **Geomorphology**

Southern Benin consists solely of sedimentary rocks from the Upper Cretaceous to the Quaternary. Its geomorphology is dominated by two series of plateaux separated by an east-west depression and by north-south valleys.

The east-west depression, called Lama, is chiefly argillaceous and flooded for part of the year (August-September). The northern plateaux, called Aplahoué, Abomey, Kétou, reach 100–150 m in altitude, with red sandy argillaceous soil and lateritic crusts. The southern plateaux, called Bopa, Allada, Sakété, rise to 20 m in the south and 90 m in the north; they consist of argillaceous, red to ochre sand, pleistocene, called 'terre de barre.' Circular depressions and small flat-bottomed valleys cut through them. The north-south valleys correspond to small rivers the Ouémé (and the So), the Kouffo (and Lake Ahémé and the Aho), the Mono (and the Sazué). These valleys have a rather varied topography viz. sandy buttes which are never covered by flood waters, low argillaceous and silty clay banks which are flooded every year, constantly hydromorphic peaty parts and open expanses of water (Lakes Aziri, Sélé, Hounhoun, Ahémé).

A coastal complex of variable width (3–5 km) lies a short distance from the ocean, consisting of old offshore bars, recent bars, depressions corresponding to former lagoons, and present-day lakes and lagoons (lagoon of Porto-Novo, Lake Nokoué, coastal lagoon).

Fig. 1A shows the geology of the southern part of Benin.

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* Ecole Normale Supérieure, 08 BP 10 Abidjan -08, Ivory Coast.

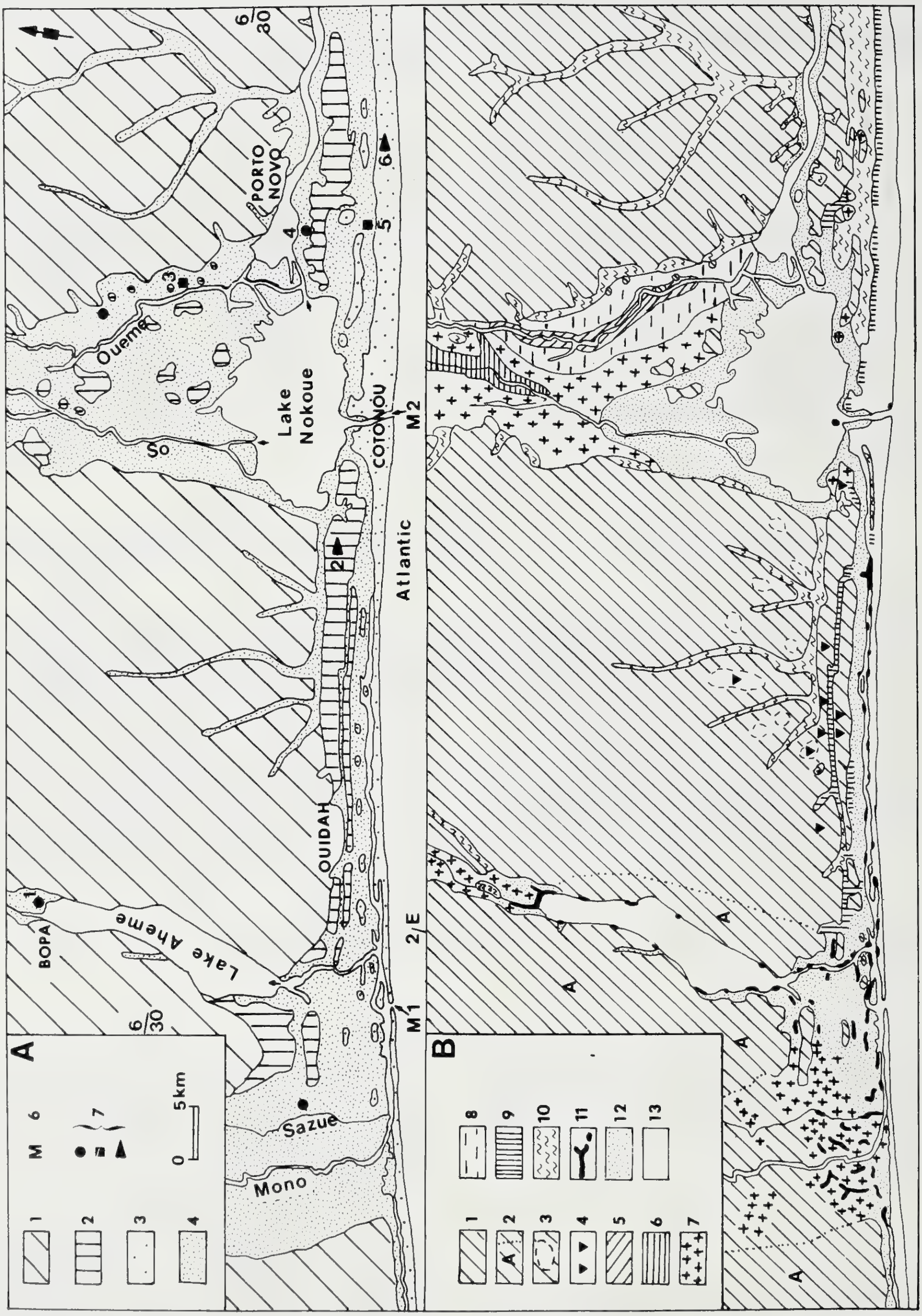

FIG. 1.—A, simplified geological map of Lower Benin. 1, 'Terre de barre' (pleistocene, argillaceous red sand); 2, yellow sand on old bars (recent pleistocene or holocene?); 3, sand of recent marine bars; 4, clay, mud and peat of valleys and depressions; 6, estuaries (entrance of salt water) with M 1 (estuary of the Mono and of the coastal lagoon) and M 2 (mouth of the channel of Cotonou); 7, organic evidence located at some depth (black circles: peat of mangrove swamps; squares: shells of brackish environment; triangles: charcoal). Number 1 was dated from 5 700 BP (GIF−2847), number 2 from 2 670 (DaK−199), number 3 from 2 670 BP (GIF−3347), number 4 from 5 430 BP (GIF−2848), number 5 from 1 050 BP (GIF−3350), number 6 from 830 BP (GIF−3973). B, schematic phytogeographic map of Lower Benin. 1, non hydromorphic formations (islands of dense semi-deciduous forest, thickets, *Elaeis* groves, fallow land in various stages); 2, *idem*, but with abundant *Adansonia digitata;* 3, savannas apparently included in past extension of dense semi-deciduous forest; 4, formations with *Lophira lanceolata* (woodlands and savannas); 5, low prairie with *Cynodon dactylon*, near the Ouémé; 6, periodically-flooded forest on the low banks of the Ouémé and So; 7, varied savannas with *Mitragyna inermis* and *Andropogon gayanus* var. *squamulatus;* 8, medium prairie with *Echinochloa pyramidalis;* 9, periodically-flooded forest (with *Symphonia globulifera*) and prairie (with *Fuirena umbellata*); 10, swampy fresh-water forests and thickets; 11, mangrove swamps; 12, prairie with *Paspalum vaginatum* (with occasional *Typha australis*); and 13, coastal vegetation (littoral thicket, littoral grassland, coconuts).

1.2 **Climate**

Southern Benin has a dry subequatorial climate with two rainy seasons and two dry seasons of unequal length: the long rainy season from April to July, the short rainy season in October, the long dry season from December to February and the short dry season in August. Two gradients characterize the region:

— a light south-north gradient with a tropical tendency with decrease in the length of the short dry season and increase in the length of the long dry season;

— a strong east-west gradient of decreasing annual rainfall (1 350 mm at Porto-Novo, 1 100 mm at Ouidah, 850 mm at Grand-Popo). Another characteristic is the great irregularity of annual rainfall from one year to the next.

The mean monthly temperatures vary little, for example Cotonou is 28°C in March, 25°C in August, with a mean temperature of 26,5°C. The maximum temperatures are close to 34°C on the coast and a little higher in the interior. The largest temperature variations occur during the days of the Harmattan (from December to February).

The dominant winds come from the south-west except during the Harmattan.

1.3 **Hydrology**

Rivers, lakes and lagoons are at their lowest depth from November to May. Most years, they are highest in September and October. Thus, in the valleys, there is an annual alternation of submersion and emersion which, with the topography, is one of the determining factors of phytocoenoses.

In the dry season, salt water from the ocean can enter the Mono River and Lake Nokoué through inlets: this explains the presence of halophytic phytocoenoses very far inland (Fig. 1B).

1.4 **Human influence**

Lower Benin appears to have been inhabited for a long time. The density of villages is high. The crops (maize, cassava, taro), the plantations (palm-oil from the last century onwards, coconut), the techniques of salt extraction (by boiling) and fishing (by placing a great number of branches in the water) and the gathering of fire wood, have brought about the destruction of forests (only a few forest islands remain) and their replacement by thickets and grassy phytocoenoses.

Man probably brought the baobab to the south-west part and very likely modified the distribution of palm trees (*Borassus* sp., *Phoenix reclinata, Raphia* spp.).

Finally, the opening of the channel of Cotonou (1885), and the construction of the Port of Cotonou (1960) have had a great impact on the environment.

As evidence of past human involvement, we were able to date with C14 some charcoal associated with neolithic quartz at Godomey* and with pottery at Kraké.**

2 PRINCIPAL PHYTOCOENOSES

2.1 **Forest islands**

2.1.1 *Dense semi-deciduous forests*

Only a few rare stands of secondary forest remain on the southern plateaux—on their slopes and in the Lama depression.

(a) *On the southern plateaux.*

The greatest number of species is found on the Sakété Plateau, with a very sharp decrease in number of species from east to west. An example of a typical forest island is that of Ké (northwest of Porto-Novo; area: 4 hectares) with the following strata and main species:

— rare megaphanerophytes (*Cola gigantea* var. *glabrescens, Ceiba pentandra, Antiaris africana, Pycnanthus angolensis* and *Triplochiton scleroxylon*);

— macrophanerophytes (*Bosqueia angolensis, Blighia unijugata, Celtis brownii, C. mildbraedii, C. zenkeri, Chlorophora excelsa, Chrysophyllum albidum, Parkia bicolor, Sterculia tragacantha, Tabernaemontana pachysiphon* and *Trichilia prieureana*);

— microphanerophytes (*Agelaea obliqua, Capparis erythrocarpos, Carpolobia lutea, Dracaena arborea, Newbouldia laevis, Oncoba spinosa, Cola millenii, Connarus africanus* and *Salacia pallescens*);

— nanophanerophytes (*Angylocalyx oligophyllus, Chassalia kolly, Cnestis ferruginea, Deinbollia pinnata, Dracaena surculosa, Mallotus oppositifolius* and *Ritchiea pentaphylla . . .*).

— lianas (*Alafia barteri, Dioscorea minutiflora, Leptoderris brachyptera, Ritchiea reflexa* and *Smilax kraussiana . . .*).

In the villages various trees which are typical of these forests can be seen. It has sometimes been assumed that all the southern plateaux were covered by a dense semi-deciduous forest (Mondjannagni, 1969), but that does not seem to be the case for the southern part of the Bopa and Allada Plateaux (Paradis *et al.*, 1978): there, the forest-savanna mosaic appears to be of long standing. Around Porto-Novo, throughout the centuries, an *Elaeis* plantation replaced the dense forest through human activity (Brasseur-Marion & Brasseur, 1953).

(b) *Lama depression (Paradis & Houngnon, 1977).* A forest expanse of 8500 hectares still exists, composed of:

— some megaphanerophytes deciduous during the dry season, over 30 m in height, and widely spaced (*Ceiba pentandra, Antiaris africana, Chlorophora excelsa* and *Triplochiton scleroxylon*);

— a continuous stratum of evergreen trees, 15–25 m in height (*Dialium guineese, Diospyros mespiliformis* and *Mimusops andongensis*), with *Afzelia africana*;

— a stratum 7–10 m in height with the same species as above but, in addition, *Celtis brownii* and *Drypetes floribunda*, and

— a very dense undergrowth (from 1–5 m tall) with *Sorindeia warneckei, Cremaspora triflora, Chassalia*

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* 2670 ± 120 BP (DaK–199)

** 830 ± 90 BP (GIF-3973) (Paradis, 1977).

kolly, Pancovia bijuga and *Gardenia triacantha* predominating.

Here and there in the forest, can be found isolated stands of *Anogeissus leiocarpus* — evidence of former land-clearing, and which must not be interpreted as relics of a southward extension of dry plant formations.

It seems likely that the clay of the entire transversal depression between the northern and southern plateaux was formerly occupied by a forest of this type. The planting of crops (maize) destroyed it almost everywhere, and today, the subsisting island, despite being theoretically a reserve, is in the process of being destroyed.

2.1.2 *Swampy fresh-water forests*

These are of two types.

(a) *In the low ground with permanently flowing water (vales of the southern plateaux, the edge of the valley of the Ouémé).* For example, the forest of the vale of Igolo, near the Nigerian border can be described (Paradis, 1975a) with:

— a discontinuous stratum 8–15 m in height (*Anthostema aubryanum, Alstonia congensis, Symphonia globulifera, Cleistopholis patens, Mitragyna ciliata, Syzygium owariense, Carapa procera, Anthocleista vogelii, Dracaena perottetii, Homalium molle, Ficus vogeliana* and *Xylopia rubescens*).

— a stratum 2–8 m tall (*Raphia hookeri, Alchornea cordifolia, Mussaenda isertiana, Sabicea africana* and *Ixora brachypoda)*;

— lianas (*Lygodium microphyllum, Canthium setosum, Eremospatha macrocarpa, Oligocodon cunliffeae, Sherbournia bignoniiflora* and *Zacateza pedicellata*);

— grasses and forbs (*Cyclosorus striatus, Impatiens irvingii, Acroceras zizanioides, Eulophia horsfalli, Brachiaria mutica* and *Palisota hirsuta*).

(b) *In the constantly flooded depressions without permanent water flow.* Such zones exist in the coastal complex and correspond to the courses of former rivers, quite evident from Cotonou to Nigeria. For example, near Krake, the forest is dominated by *Ficus congensis* with *Anthocleista vogelii, Syzygium owariense, Chrysobalanus ellipticus.* Only during the flood season (August to November) does the water flow freely. The rest of the year it is stagnant.

In such an environment, a *Ficus congensis* forest can be found in the old course of the Kouffo to the north of Lake Ahémé.

Man has had an influence on the swampy forests, by cutting down tall trees with straight trunks (*Alstonia, Cleistopholis, Mitragyna* and *Symphonia*), by planting *Raphia* palms to be used in various ways, by penetrating into the clearings to harvest species of forbs (*Thalia welwitschii, Cyrtosperma senegalense*), the leaves of which are used to wrap food sold in the markets. In the Ouémé Valley, taro is grown at the site of a swampy forest which was almost entirely cleared away for that purpose. Now, in that valley, rice-growing, through the extension of draining, is modifying the environment. The final result of human influence is an abundance of thickets and marshy prairies with a few scattered, tall trees.

2.1.3 *Periodically-flooded forests*

They are of three types, according to the substrate (Paradis, 1975a, 1975b; Berding, 1976).

(a) on the low banks of the Ouémé and the So. To the north of Adjohoun, along the edge of these two rivers, made up of silty argillaceous soil, a riverbank forest lies on the low banks, forming a veritable gallery forest. It is inundated during the flood season for one to two months a year. Its composition is as follows:

— a stratum of trees (8–12 m) with *Afzelia africana, Cynometra vogelii, Dialium guineese, Lonchocarpus sericeus, Manilkara obovata* and *Pterocarpus santalinoides;*

— a stratum of shrubs with *Cola laurifolia, Memecylon blakeoides* predominating and *Mimusops kummel, Mitragyna inermis, Morelia senegalensis, Pachystela brevipes* and *Pavetta owariensis*;

— lianas: *Flagellaria guineensis, Leptoderris brachytera* and *Paullinia pinnata.*

— a herbaceous stratum with *Crinum jagus, Haemanthus rupestris, Amorphophallus atrovirens, Herderia truncata* and *Hypolytrum poecilolepis.*

(b) *On the sand along the edge of the depressions of the coastal complex.* Here, the level of phreatic water fluctuates throughout the year, rising to one metre above ground from June to November, and falling to one metre below during the dry season. Such an environment is occupied by forest in which *Symphonia globulifera* is abundant, along with such species as *Cleistopholis patens, Alstonia congensis, Memecylon blakeoides, Anthocleista vogelii, Berlinia grandiflora, Syzygium guineese, Chrysobalanus ellipticus* and *Ancistrophyllum secundiflorum.*

Man has, in many places, tranformed this forest into *Elaeis* groves and grass savanna with *Loudetia phragmitoides* and *Panicum congoense* (Paradis, 1975a).

(c) *On the sandy islets of the Ouémé Valley.* Here there are occasionally-flooded forests, comprised of a mixture of riverbank forest species such as *Cynometra vogelii, Cola laurifolia, Lonchocarpus* spp., *Manilkara obovata, Ostryocarpus riparius* and *Pterocarpus santalinoides* and semi-deciduous forest species such as *Ceiba pentandra, Cola gigantea* and *Cola millenii.*

2.1.4 *Woodlands with* Lophira lanceolata

In the Ahozon Reserve, on yellow sand, *L. lanceolata* forms a monospecific, 6–10 m-high, closed community with a single stratum. The herbaceous plants, well-developed in October, include a stratum, 1–1,3 m high, with *Ctenium canescens, C. newtonii, Setaria pallide-fuscae* and *Schizachyrium sanguineum* and a lower stratum with Cyperaceae like *Bulbostylis aphyllantoides, Kyllinga erecta* and *Cyperus margaritaceus.* Almost everywhere, these woodlands have been tranformed into tree and shrub savannas invaded by small thickets (see below).

2.1.5 *Mangrove swamps (Paradis & Adjanohoun, 1974; Paradis, 1979, 1980, 1981)*

At some points (north-west of Lake Ahémé, east of the coastal lagoon, between the Aho and Grand-Popo) there remain some relics of a mangrove swamp with *Avicennia africana* and *Rhizophora racemosa*, formerly more extensive. Between Ouidah and the estuary, on the areas degraded for the extraction of salty soil, there are some small populations of *Laguncularia racemosa*.

2.2 **Thickets, savannas, prairies, grasslands and floating vegetation**

2.2.1 *Thickets*

(a) *Littoral thicket (Paradis, 1976; Souza, 1979).* In rare places on the coast there remain patches of this thicket with shrubs *(Manilkara obovata, Fagara zanthoxyloides, Diospyros tricolor, Syzygium guineense* and *Chrysobalanus orbicularis),* liana *(Sarcostemma viminale)* and a geophyte *(Sansevieria liberica).* In addition, there is the occasional *Adenia lobata, Agelaea obliqua, Carissa edulis, Chassalia kolly, Flacourtia flavescens, Ritchiea reflexa, Trema guineensis,* and *Phoenix reclinata.* It seems likely that this coastal thicket constituted the edge of a littoral forest with *Manilkara obovata,* destroyed for the extraction of salt by boiling sea water.

(b) *Thicket with* Dalbergia ecastaphyllum *(Paradis, 1979).* This species is abundant in readily-flooded parts on the banks of the coastal lagoon, where it is often associated with *Drepanocarpus lunatus,* in the clearings of *Rhizophora* mangrove swamp, and along depressions with *Typha australis* and *Kyllinga peruviana* of the coastal sand. This thicket, 2–4 m in height, is not easily penetrated, and constitutes a phytocoenose of long duration. At the edge of the mangrove swamp, it impedes the reconquest of the environment by *Rhizophora* and *Avicennia.*

(c) *Thicket on yellow sand and 'terre de barre.'* On yellow sand, scattered among the *Lophira lanceolata* formations, thickets 6–12 m in height and 10–100 m in diameter are plentiful. Their flora, which is quite abundant, includes *Barteria nigritiana, Bridelia ferruginea, Dialium guineense, Fagara zanthoxyloides, Annona senegalensis, Byrsocarpus coccineus, Carissa edulis, Cnestis ferruginea* and *Vitex doniana.* The majority of these species are zoochorological (ornithochore and cheiropterochore). These thickets are a stage in the progression of *Lophira* savanna to forest: one can often observe rotting trunks of *Lophira* in the thickets.

On 'terre de barre,' likewise, there is a thicket formed by numerous discontinuous copses more or less extensive, 4–8 m in height. The tallest trees are *Bridelia ferruginea, Fagara zanthoxyloides, Malacantha alnifolia, Phyllanthus discoideus* and *Vitex doniana.* They tower over a number of small shrubs. Here, these thickets are undoubtedly a stage in the progression of old savannas to forest (Paradis *et al.*, 1978).

(d) *Wooded thicket at the edge of the Lama Forest.* This thicket clearly results from the invasion of savanna by forest. Indeed, it is comprised of:

— large savanna trees, from 5–12 m in height, widely spaced (*Anogeissus leiocarpus, Combretum molle, Fagara zanthoxyloides, Lannea kerstingii, Piliostigma thonningii, Pterocarpus erinaceus* and *Terminalia glaucescens)*;

— a closed stratum, from 0–5 m in height, with the same floristic composition as that of the Lama Forest with much *Dialium guineense, Diospyros mespiliformis, Mimusops adongensis* and *Celtis brownii.* The diameter of these forest species is small. This wooded thicket on the forest periphery appeared after the area was made a reserve, which put a stop to annual fires. As long as fires occurred each year, the savanna species grew without competition but, as soon as they stopped, the forest species, better adapted to the present environment, were able to occupy the former burnt sites.

2.2.2 *Tree savannas and shrub savannas*

(a) *With* Terminalia glaucescens *of the Lama depression and north of Lake Ahémé.* These are Guinean savannas with numerous species, but without *Lophira lanceolata* or the Shea butter tree. It is possible that these savannas have arisen through the destruction of woodlands by man.

(b) *With* Lophira lanceolata. These result from deterioration of the *Lophira* woodlands. Their floristic composition is the same as that of the woodlands.

(c) *With* Mitragyna inermis *and* Phoenix reclinata (*in the valleys*). In the Ouémé valley, this savanna is characterized by a tree stratum (with *Mitragyna inermis* and some *Pterocarpus santalinoides*), a shrub stratum (with *Antidesma venosum, Drepanocarpus lunatus,* small *M. inermis, Mimosa pigra* and *Vitex doniana)* and an herbaceous stratum (with *Andropogon gayanus* var. *squamulatus, Axonopus flexuosus, Cyperus articulatus, Eriosema glomeratum, Hibiscus asper* and *Hygrophila auriculata).* In some scattered spots there are copses with *Phoenix reclinata.* In the valleys of the Kouffo and the Mono, these palm-trees are abundant, and in the south-west there is also *Borassus aethiopum.* Near Cotonou and in the south-east there are some dispersed stands of *M. inermis.*

These *M. inermis* savannas occur on soil which is seasonally flooded and composed of clay or silty-argillaceous sand. They appear to have been derived under the influence of fire, from riverside forests.

2.2.3 *Grass savannas and varied prairies*

These low phytocoenoses, with superficial roots, can be classified according to the characteristics of the substratum.

(a) *On sand never or rarely flooded:*

— on 'terre de barre' grassy savanna with *Andropogon tectorum* and *Imperata cylindrica,* characteristic of exhausted soils, which become very sandy;

— on yellow sand grassy savanna with *Ctenium newtonii* and *Schizachyrium sanguineum,* resulting from the great deterioration of *Lophira* shrub savannas.

(b) *On sand periodically flooded:*

— littoral zone: the highest areas are occupied by a prairie with *Vetiveria nigritana*, the lowest points are covered by a prairie with *Panicum congoense* (Guinko, 1974), the places, topographically very low, by a prairie with *Loudetia phragmitoides;*

— low Ouémé valley: the bulge of the steep river bank, silty and sandy, is occupied by a low *Cynodon dactylon* prairie, used very much for grazing, with numerous ruderal species. In flood season, this bulge is inundated almost every year and invaded by floating vegetation;

(c) *On argillaceous and silty clay soil, periodically flooded:*

— littoral zone (in the depressions parallel to former bars): medium prairie with *Fuirena umbellata;*

— low Ouémé valley: medium prairie with *Echinochloa pyramidalis* and *Brachiaria mutica* (and during the dry season *Aeschynomene indica, Digitaria horizontalis, Hyptis lanceolata, Paspalum orbiculare* and *Pentodon pentandrus*). During the flood season, most of these species become floating. In addition, there are some Cyperaceae (*Cyperus haspan. Fuirena umbellata* and *Rhynchospora corymbosa*), and various strictly floating species.

(d) *On substrata saturated with fresh water all year long:*

— high prairie with *Typha australis* (with very few species: *Paspalum vaginatum,* where the salinity increases during the dry season, *Polygonum pulchrum, Cyperus papyrus, Cyclosorus striatus* and *Cyrtosperma senegalense* where the water remains fresh all the time). Such a prairie is located around the lagoon of Porto-Novo (Paradis & Rabier, 1979), between Cotonou and the eastern limit of the mangrove swamp, in the abandoned meanders of the Kouffo (north of Lake Ahémé), and in the depression between the Allada plateau and the yellow sand (from Pahou to Godomey);

— a community of *Cyperus papyrus,* which is not very extensive (behind the preceding community where the water is acid) with *Phragmites australis* and *Echinochloa pyramidalis;*

— a community with *Nymphaea lotus* in the numerous expanses of open water;

— a community with *Cyclosorus striatus,* very extensive on the periphery of Lakes Aziri and Hounhoun, and in the gaps of swamp forests. This fern floats during floods. The death of the fern, without decomposition of its rhizome, produces floating peat on which seeds from trees of swamp forests can germinate;

— a community with *Pycreus mundii,* localized in one spot (Guinko, 1974).

(e) *On hydromorphic substrata, slightly brackish at certain times of the year.* On these substrata there occur an *Eleocharis* spp. prairie behind the mangrove swamps (from Ouidah to Togbin), and a community behind the offshore bar (between it and the mangrove swamps) with *Kyllinga peruviana, Phyla nodiflora, Fimbristylis obtusifolia, Mariscus ligularis, Pycreus polystachyos, Hydrocotyle bonariensis* and *Philoxerus vermicularis.*

(f) *On a salty substratum (Paradis, 1980):*

— grassland with *Sesuvium portulacastrum* and *Philoxerus vermicularis* on the periphery of areas where salty earth is extracted (south-western region).

— low prairie with *Paspalum vaginatum,* very extensive (Fig. 1B), and with other species (*Cyperus articulatus, Bacopa crenata, Pentodon pentandrus* and *Pycreus polystachyos*). Occasional clusters of *Acrostichum aureum* can be found scattered over the prairie.

— littoral grassland with two features (in the low areas, on prograding, sand, pioneer vegetation with *Ipomoea pes-caprae, Remirea maritima* and *Cyperus maritimus;* in the high areas of the offshore bar, grassland with *Sporobolus virginicus, Schizachyrium pulchellum, Ipomoea stolonifera* and *Diodia vaginalis,* with small dunes having scattered *Scaevola plumieri*).

2.3 **Floating vegetation (Paradis & Rabier, 1979; Texier *et al.*, 1980)**

Floating vegetation begins to multiply rapidly when floods occur in the low valleys. On the lagoon of Porto-Novo, they constitute floating islands with:

— species floating freely on the surface: *Azolla africana, Salvinia nymphellula* and very abundant *Pistia stratiotes;*

— immersed species: *Ceratophyllum demersum;*

— species with creeping stems which can live rooted on the edge of banks: *Aeschynomene indica, Commelina congesta, Enydra fluctuans, Ipomoea aquatica, Jussiaea repens* var. *diffusa, Leersia hexandra, Marsilea diffusa;*

— helophytic species: *Echinochloa pyramidalis, Cyperus papyrus, Typha australis, Paspalum vaginatum, Polygonum pulchrum.* Due to its great biomass, this category gives its physiognomy to the floating islands.

In the lagoon of Porto-Novo the floating vegetations spreads from January onwards following an increase in salinity. It begins to take over the lagoon in June-July.

CONCLUSIONS

This phytogeographic overview of Southern Benin shows the great variety of phytocoenoses caused, on the one hand, by climatic, topographic and edaphic factors and, on the other, by human influence on the environment. The result is a mosaic of plant formations in which thickets and savannas of several types predominate.

The natural historical factors, especially paleoclimate, have not yet been elucidated.

Future research should focus on detailed cartography, to a scale of 1: 50 000 (already begun), on the determination of kinds of charcoal (in collaboration with archaeologists) and on the palynological study of soil samples.

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Comments on primitive South African crop sorghums and the evolution of sorghum races in Africa

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ABSTRACT

In recent years considerable research has been carried out on cultivated *Sorghum bicolor* (L.) Moench in an attempt to acquire a more complete and meaningful understanding of the taxonomy, classification, origin and evolution of Africa's most valuable cultivated crop. This work has, however, been restricted mainly to the sorghums in northern and central Africa, with southern Africa largely excluded.

In this paper, the morphological variation and distribution of cultivated sorghum races in South Africa is introduced, together with comments on the classification of cultivated sorghums. A new morphological character, the groove at the base of the lower glume of mature, sessile spikelets (developed from a zone of weak, membranous tissue observable in immature spikelets) is evaluated. The degree of development of this groove varies between the different races and is considered to relate directly to their evolution and domestication.

RÉSUMÉ

COMMENTAIRES SUR LES SORGHOS CULTIVÉS D'AFRIQUE DU SUD ET SUR L'ÉVOLUTION DES RACES DE SORGHUM EN AFRIQUE

Durant les récentes années, une recherche considérable a été menée sur le Sorghum bicolor *(L.) Moench en vue de tenter d'acquérir une compréhension plus complète et significative de la texonomie, la classification, l'origine et l'évolution de la culture la plus importante de l'Afrique. Ce travail a cependant été limité principalement aux sorghos du nord et centre de l'Afrique, l'Afrique australe étant en grande partie exclue.*

Dans ce document, la variation morphologique et la répartition des races de sorghos cultivés en Afrique du Sud sont introduites, avec des commentaires sur la classification des sorghums cultivés. Un nouveau caractère morphologique, le sillon à la base de la glume inférieure des épillets sessiles mûrs (développé à partir d'une zone de tissus membraneux faibles pouvant être observée sur les épillets non mûrs) est évalué. Le degré de développement de ce sillon varie entre les différentes races et est considéré comme directement apparenté à leur évolution et domestication.

INTRODUCTION

The last significant input into taxonomic research on South African crop sorghums was made forty-five years ago by Snowden (1936) as part of his world monograph on the group. In more recent years, the importance of sorghum germ plasm and the need for a better and more complete understanding of the morphology, origin, evolution and classification of cultivated sorghums has led to renewed research interest in them. This research, however, has been concentrated around the region of early sorghum domestication of northern and central Africa, to the almost complete exclusion of the crop in southern Africa.

In this paper an attempt is made, at least in part, to update our knowledge of South African sorghum cultivates, and to bring it into line with research undertaken elsewhere in Africa. Morphological and geographical information presented is by no means complete. It is merely offered as an introduction to an extensive survey currently being undertaken on southern African crop sorghums.

In the latter half of the paper the evolution and early migration of cultivated sorghums are discussed. The conclusions presented are based largely, although not exclusively, on a study of southern African material, and are therefore to some extent speculative. To make this work more meaningful and acceptable, there is a need for these conclusions to be more fully tested against material from elsewhere in Africa.

MORPHOLOGICAL VARIATION

Primitive crop sorghums in South Africa exhibit a wide range in morphological variation. According to De Wet & Huckabay (1966), De Wet & Harlan (1971), De Wet *et al.* (1972) and De Wet (1978), only three races of cultivated sorghum are grown in this region: namely, races Bicolor, Guinea and Caffra. As a result of this investigation, it is now known that all five sorghum races (races Caudatum and Durra included) are cultivated in varying proportions in South Africa. Furthermore, the members of these races hybridize freely and introgress with each other, producing a number of intermediate races.

Race Bicolor (Fig. 1): This race, which most closely resembles the wild sorghums, has a primitive spikelet morphology and is considered to be the least specialized of all the cultivated sorghum races (Harlan & De Wet, 1972; Harland & Stemler, 1976). The inflorescence is characteristically open and paniculate, but may also be subumbellate. The glumes are long (lower: 4,3–5,7 mm; upper: 4,0–5,6 mm) exceeding the grain in length. At maturity they tightly clasp the grain, exposing only its apex. They are mostly smooth and shiny and vary in colour from beige to dark brown, maroon-red and black. The weak membranous zone and basal groove

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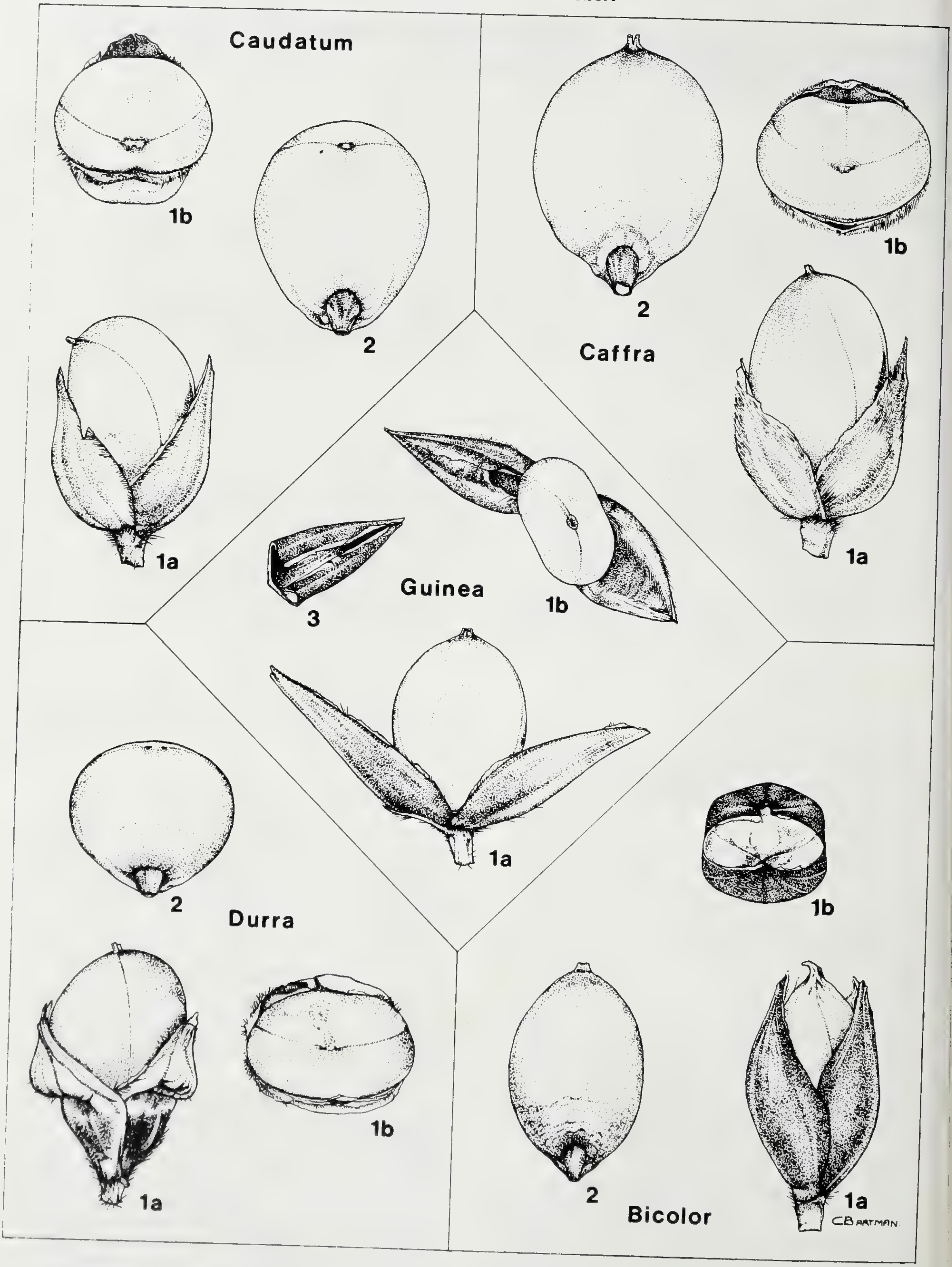

FIG. 1.—Spikelet and grain morphology. 1a & 1b, mature spikelet (a, longitudinal view, b, dorsal view); 2, mature grain (longitudinal view); 3, part of lower glume illustrating turned margins (race Guinea).

(discussed later in this paper) are absent from the lower glume, except where introduced through hybridization and introgression with other races. The grain is relatively small (3,9–4,6 × 2,2–3,1 mm), linear-elliptical in shape and varies in colour from cream to orange-yellow or brown with the exposed apex usually a dark brown or red-brown.

Race Guinea (Fig. 1): Despite its many specialized characters, this race is most closely related to race Bicolor, possessing in common with it the open inflorescence, long glumes and sweet stems. The inflorescence is characteristically open with the branches frequently drooping (pendular). Subumbellate forms have also been recorded. The glumes are long (lower: 4,3–5,0 mm; upper: 4,1–5,2 mm) and exceed the grain in length. At maturity they open and gape, especially the upper glume, the margins of which become strongly inturned. The glumes are generally smooth and shiny, with a limited pubescence, and range in colour from cream-beige to purple, red and black. The zone of weakness and basal groove are present on the lower glume, but are not as broad as in races Caffra and Caudatum. Grain shape is elliptical to discoid (3,3–4,1 × 2,4–3,3 mm). The grains are mostly white coloured with cream and beige-brown grained forms also observed. They are characteristically turned between the glumes, mostly between 55° and 86°. Turning is obstructed in some spikelets due to the grains being tightly clasped by the margins of the lower glumes. Because of the gaping nature of the glumes, the grains are highly exposed and easily dislodged from the spikelet at maturity.

Race Caffra (Fig. 1): In this race the inflorescence may be open or highly compacted, with the majority of individuals having loosely compacted inflorescences which are cylindrical in outline. The glumes are notably shorter than the grain (lower: 3,1–4,4 mm; upper: 3,5–4,5 mm), which they firmly clasp, exposing the upper ½–⅓ of its upper surface. They are smooth and often highly pubescent, giving the spikelet a dull appearance. Glume colour ranges from cream to beige, brown, purple, maroon and black. The zone of weakness and basal groove are highly developed in this race. At maturity the lower glume is distinctly shorter than the upper glume, due to it folding back on itself at the zone of weakness, located at the base of the lower glume. The grains are obovoid to elliptical in shape (3,7–4,8 × 3,0–4,5 mm) with rounded (oval) grains also observed. The colour range is considerable, varying from white to cream, cream-yellow, orange, light and dark brown and red. In the majority of inflorescences examined, between 1–10% of the grains were turned between the glumes, up to a maximum of 58°. This suggests a relatively high incidence of crossing having taken place between races Guinea and Caffra.

Race Caudatum (Fig. 1): Caudatum sorghums closely resemble members of race Caffra, and are considered to have evolved from early members of this race. The inflorescence is loosely or tightly compacted. The glumes, typically black in colour, are shorter in length than the grains (lower: 3,1–4,5 mm; upper: 3,3–4,5 mm), which they firmly clasp, exposing the upper ½–⅓ of the grain surface. The glume surface is smooth and usually pubescent giving the spikelet a dull appearance. The black colour of the glumes contrasts strongly with the predominantly white grains. The zone of weakness and basal groove are well developed as in race Caffra. This race is characterized by an asymmetrical grain, rounded on the inside (back) with the style base displaced out and downwards from the grain apex to a lateral position near the apex of the lower glume, giving the grain a typically 'hunchback' appearance. The grains are obovoid or broadly obovoid in shape (3,7–4,2 × 3,4–4,0 mm). As with race Caffra, many of the inflorescences have grains that rotate between the glumes.

Race Durra (Fig. 1): This race is markedly distinct from other cultivated sorghum races. The inflorescence varies between compact and loosely compact. The glumes are shorter than the grain (lower: ±4,0 mm; upper: 4,0–4,1 mm), exposing the upper half of its surface. Both glumes have a transverse medial crease or fold which characterises this race. Below the fold the glume is hard and cretaceous while the upper half is normally soft and leathery. The cream-orange grains are large (4,1 × 4,3 mm), and obovoid in shape with a broad somewhat flattened apex and triangular base. The basal groove and zone of weakness associated with the lower glume in most other races is absent in this race.

Intermediate races: Intermediate forms between the different races are common, often exhibiting a continuous range in variation between parent races. De Wet (1978) recognizes three intermediate races from South Africa, which are synonomous with four of the cultivated *Sorghum* species recorded from this country by Snowden, namely:

1. Caffra × Bicolor = *S. basutorum*
2. Bicolor × Guinea = *S. millitium*, and *S. roxburghii*
3. Bicolor × Durra = S. *subglabrescens*

An additional four intermediate races have been identified during this study.

4. Caffra × Guinea
5. Caffra × Caudatum
6. Bicolor × Caudatum; and
7. Guinea × Caudatum.

Besides the usual two way crosses, a few plants have been observed which exhibit a combination of characteristics from three races, namely, races Caffra × Caudatum × Bicolor. The typical characters of each race may or may not necessarily be equally well represented in the compound intermediate form.

DISTRIBUTION

No attempt is made by Snowden (1936) to outline the distribution of the eight species of cultivated sorghum recorded by him for South Africa. He merely cites specific localities where these are known. This is understandable due to the limited amount of South African material at his disposal which does not lend itself to accurate geographical extrapolation. The most recent accounts of cultivated sorghum distributions in South Africa are by De Wet & Huckabay (1966), De Wet & Harlan (1971), and De Wet *et al.* (1972 & 1976), all of whom appear to have based their distributions of cultivated South African sorghums largely on Snowden's (1936) outdated work. It is impossible at this stage of the current investigation of cultivated South African sorghums to give an accurate updated account of their distribution, as only part of the region has been sampled to date and in many cases in insufficient detail. The distributions oulined below are therefore incomplete, but do, nevertheless, give a more realistic account of the situation than is available in existing literature.

Race Caffra: This is grown purely as a grain sorghum, and is the most widespread and abundant race in South Africa. It is known to be cultivated in northern Namibia (South West Africa), northern and eastern Botswana and the entire eastern half of South Africa.

Race Guinea: This race is grown equally for its sweet stems and grain. It is slightly less widespread and less commonly grown than race Caffra. Its distribution extends from the northern and eastern Transvaal, through Swaziland to northern Natal (Zululand).

Race Bicolor: Members of this race are cultivated almost exclusively for their sweet stems. They are generally less commonly grown than the two former races. The distribution includes northern Namibia, the south-western Transvaal (Bophuthatswana), the north-eastern Transvaal (Venda) and north-western Transvaal (Lebowa).

Race Caudatum: This race has not previously been recorded from South Africa. It is not as abundant as races Caffra, Guinea or Bicolor. Its current distribution includes collections from various localities throughout Venda and only one collection from Lebowa. Caudatum sorghums lack the sweet stems of Bicolor and Guinea sorghums and are therefore grown exclusively for their grain.

Race Durra: Previously unrecorded from South Africa except for *S. subglabrescens* (Snowden, 1936) regarded by De Wet (1978) as an intermediate race between races Bicolor and Durra. Only two collections have been made to date, both from a single village in Venda. It is cultivated exclusively for its grain.

CLASSIFICATION

Until recently, Snowden's (1936) classification was used almost exclusively for South African crop sorghums. This classification is far from satisfactory, but with nothing better to take its place, is still in use. Its many shortcomings are outlined by Harlan & De Wet (1972). The most realistic treatment of cultivated sorghums to date is that of De Wet & Huckabay (1966) and De Wet (1978). Their biological species approach is practical and particularly well suited to crop plants, and provides an acceptable solution to the problems encountered in cultivated sorghum classification. This system of classification, which was later extended by Harlan & De Wet (1971) to include all cultivated plants, is not, however, exempt from criticism. In this regard support is given to the comments made by Westphal (1974).

The division of a species, containing both wild and cultivated members, into two subspecies is unacceptable as it clashes directly with the use of subspecies in conventional taxonomy, and disregards geographic separation as a delineating criterion. Remoulding of the subspecies concept, as Harlan & De Wet (1971) have done, to accommodate cultivated plants strongly contradicts their support for Jeffrey (1968) who proposed that formal botanical categories and nomenclature should not be used for cultivated plants at the infraspecific level. It also contradicts their decision not to use variety as a botanical term for cultivated plants, on the grounds that this would cause confusion. The need to distinguish between cultivated and wild taxa within a single species is not totally without support. It is considered undesirable, however, to do this by creating a special category.

No immediate objection can be found for using race and subrace as infraspecific ranks for cultivated plants. The recognition of a fifth taxonomic rank below that of cultivar, namely, line, clone and genome, is contrary to the code which designates cultivar as the lowest category for cultivated plants.

The concept of race as defined by Harlan & De Wet (1971) represents a hybridization of the formal taxonomic categories subspecies and variety, and is considered suitable as the basis for the initial grouping of cultivated plants within a species. Similarly, subrace is seen as an acceptable means by which to identify convenient divisions within each race. The use of race and subrace, by Harlan & De Wet, as subdivisions for infraspecific wild taxa is unjustified. Not only is it contrary to the Code, but also attempts to destroy part of a generally accepted system which has been in use for a considerable period of time. Furthermore, and perhaps even more important, it is not seen as an improvement over the system currently in use. It seems strange that these authors, who support not using formal taxonomic categories for cultivated plants, can at the same time promote the idea that categories created by them for cultivated plants are suitable for use with wild taxa.

NEW SUPPORTING EVIDENCE

This study of cultivated sorghum races in southern Africa has brought to light a new character which supports the conclusions of De Wet & Harlan (1971), De Wet *et al.* (1972 & 1976), Stemler *et al.* (1975), De Wet (1978) and Harlan & Stemler (1976) regarding the evolution and early movement of cultivated sorghum races in Africa.

The character presents itself in two forms depending on the age of the spikelet (Fig. 2). In the immamature, sessile spikelet it exists as a thin membranous zone situated at the base of the lower (outer) glume. In the mature spikelet it is seen as a groove at the base of the glume. Both the membranous zone and the groove are differentially developed in the different races, being absent in race Bicolor and Durra, well developed in Caffra and Caudatum and intermediate in race Guinea. It should be pointed out that all reference to these characters and the extent to which they are developed in the different races is directed strictly at the typical forms within each race. Because of hybridization and introgression, individuals have been observed in which this character is atypical of the race in which they are naturally placed. In most of these cases, however, the intermediate nature of the plants can be determined.

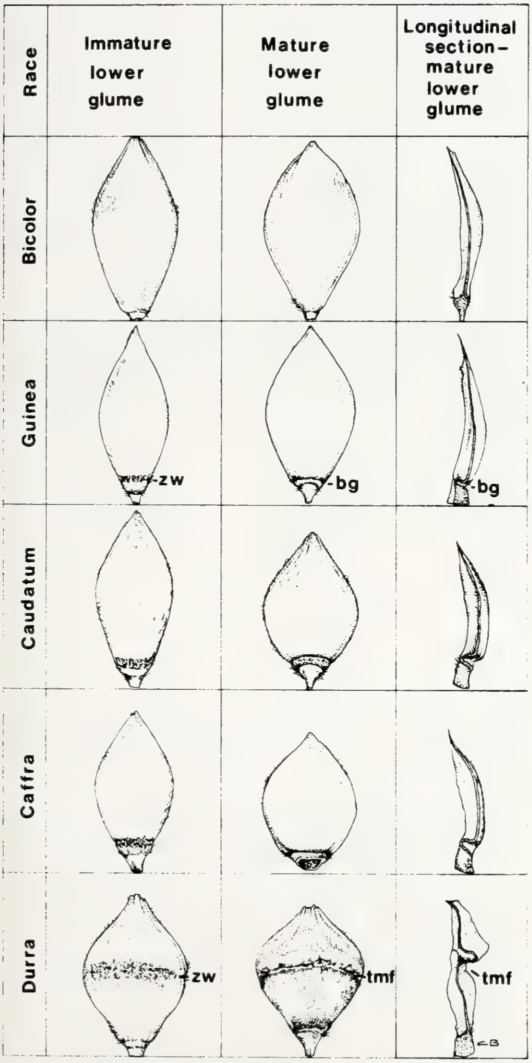

FIG. 2.—Structure of lower glume. zw, zone of weakness; bg, basal groove; tmf, transverse medial fold.

DEVELOPMENT OF THE BASAL GROOVE

The basal groove is located at the base of the lower glume of the mature fertile spikelet. It is not present on the upper glume. It develops from the weak membranous zone of tissue present in immature spikelets. As the grain matures and swells the lower glume, as it is pushed outwards, folds back on itself along the zone of weakness resulting in the formation of the basal groove. The zone of weakness is hidden in the mature spikelet inside the groove and is often further obscured by the long hairs concentrated at the glume base. The effect of the formation of the groove is to shorten the apparent length of the lower glume. This is particularly pronounced in races Caffra and Caudatum (Fig. 2).

SELECTIVE ADVANTAGE OF THE ZONE OF WEAKNESS

The presence and degree of development of the zone of weakness is considered to have arisen as of a direct selective response to domestication, the advantage of which is realized during the threshing of the grains.

In race Bicolor (Fig. 1) the glumes of the fertile spikelet tightly clasp the grain. This condition is disadvantageous during threshing as it prevents easy separation of the grain from the spikelet. Furthermore, it would also result in an increased incidence of shattering of the grains due to prolonged and more intensive stamping needed to dislodge the grain during threshing. Shattered grains are highly undesirable as the small fragments are difficult to separate from the chaff during winnowing. Race Bicolor is cultivated largely for its sweet stems rather than for its grain. In South Africa it is grown almost exclusively for this purpose. Selection favouring threshing is therefore minimal and would account for the zone of weakness being absent in the typical forms of this race.

In races Guinea, Caffra and Caudatum, which are cultivated primarily for their grain, threshing is made easier by the presence of the zone of weakness. During threshing the lower glume breaks away from the spikelet along the weak membranous tissue at its base, enabling the grain to be more readily separated from the spikelet.

The extent to which the zone of weakness is differentiated in these races can also be correlated with threshing. In race Guinea (Fig. 2) the membranous zone although present is not as broad as in race Caffra or race Caudatum. This is considered to be due to Guinea sorghums having evolved in the wetter, more humid environment of West Africa. In this race the inflorescence branching has remained open and specialization has produced fertile spikelets with glumes that open and gape together with discoid grains that turn between the glumes. These are important adaptations enabling the inflorescence and spikelets to dry out more easily in the wet West African climate. This specialization strongly favours easy separation of the grains from the spikelet during threshing, and would, therefore, have negated any further need for the zone of weakness continuing to develop.

The zone of weakness is best developed in races Caffra and Caudatum (Fig. 2). In these races the glumes firmly clasp the lower portion of the grain. A well-developed zone of weakness is therefore desirable in order to facilitate easy grain removal during threshing. Release of the grain may also be helped by the shortness of the glumes in these two races.

The absence of the zone of weakness at the base of the lower glume in race Durra, adds support to an independent origin of this race from primitive Bicolor sorghums. In Durra sorghums separation of the grain during threshing is helped by the transverse medial folds on each glume (Fig. 2). These folds are equivalent to the basal groove in other races, and develop from zones of thinner, weaker tissue present on both glumes of the fertile spikelet. During threshing the upper halves of the glumes would break away at these zones thus enabling easier release of the grains from the spikelets.

EVOLUTION AND EARLY MOVEMENT

A schematic outline illustrating the lines of evolution and specialization of the five cultivated sorghum races is presented in Fig. 3. The wild progenitors of cultivated sorghums are believed to be members of *S. bicolor* subsp. *arundinaceum,* either from race Aethiopicum or race Verticilliflorum or possibly from a complex involving both these races (De Wet, 1976).

Cultivation of the wild progenitor led to the origin of a primitive Bicolor cultivate (Fig. 3–A), characterized by non-articulating spikelets and enlarged grains (De Wet *et al.,* 1972). Primitive Bicolor sorghums are considered to have given rise to two distinct evolutionary lines. The first line (Fig. 3–B1) includes race Durra, considered by Harlan and Stemler (1976) to have evolved in Asia independently of the other sorghum races, and later reintroduced back into Africa (Fig. 4–2). Race Durra is distinct from other sorghum races, particularly in the size and form of the grains and the transverse medial folds across both glumes of the fertile spikelet. It is considered to be linked somewhat distantly to race Bicolor through primitive Bicolor sorghums. These two races share in common the absence of the zone of weakness and groove at the base of the lower glume.

The second line of evolution from primitive Bicolor (Fig. 3–B2) is responsible for producing the four remaining sorghum races. The most primitive and least specialized of these is race Bicolor, which has probably changed little from the original primitive Bicolor stock. At an early stage in its development, some of its members developed the zone of weakness on the lower glume. This character, because it is present in both Guinea and Caffra sorghums, is considered to have originated before primitive Bicolor was moved to West and southern Africa (Fig. 4–1a & 1b).

This specialized form of primitive Bicolor is considered to be the progenitor of two independent lines of evolution. Firstly it gave rise to race Guinea (Fig. 3–C1), which is generally accepted as having evolved in West Africa (Fig. 4–3). Specialization in

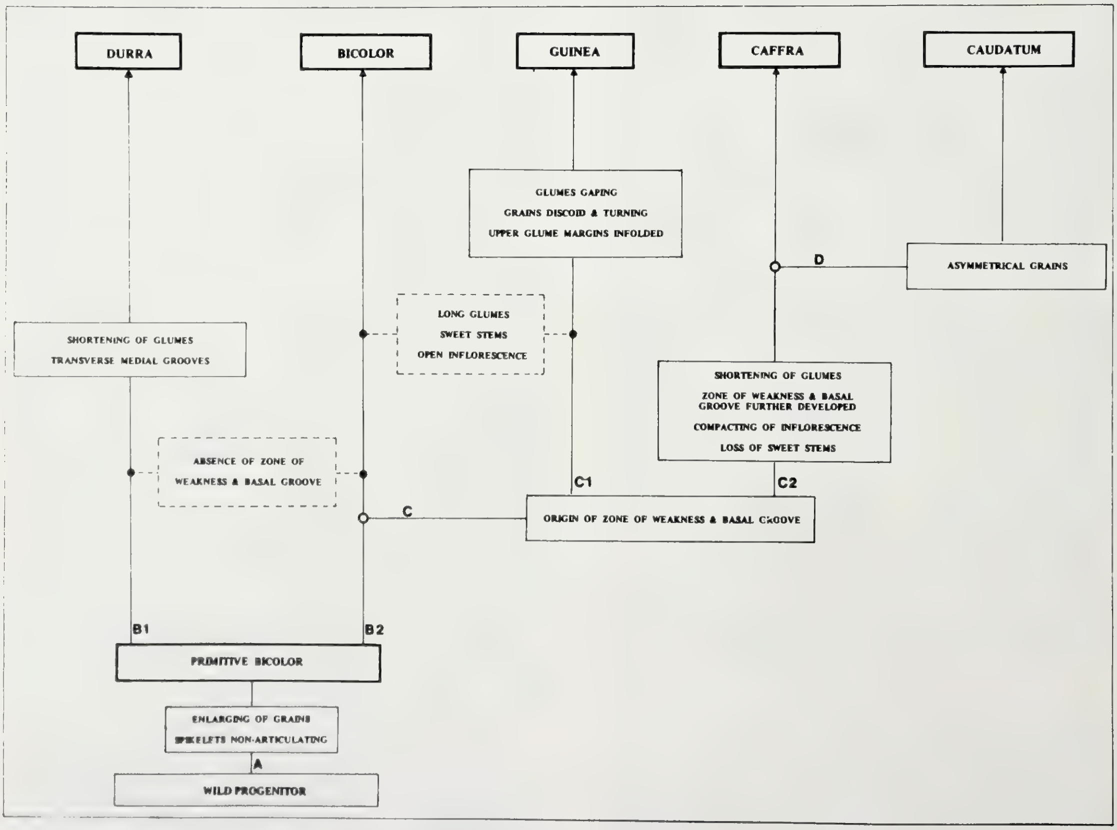

Fig. 3.—Schematic outline illustrating lines of evolution and specialization of the five cultivated sorghum races.

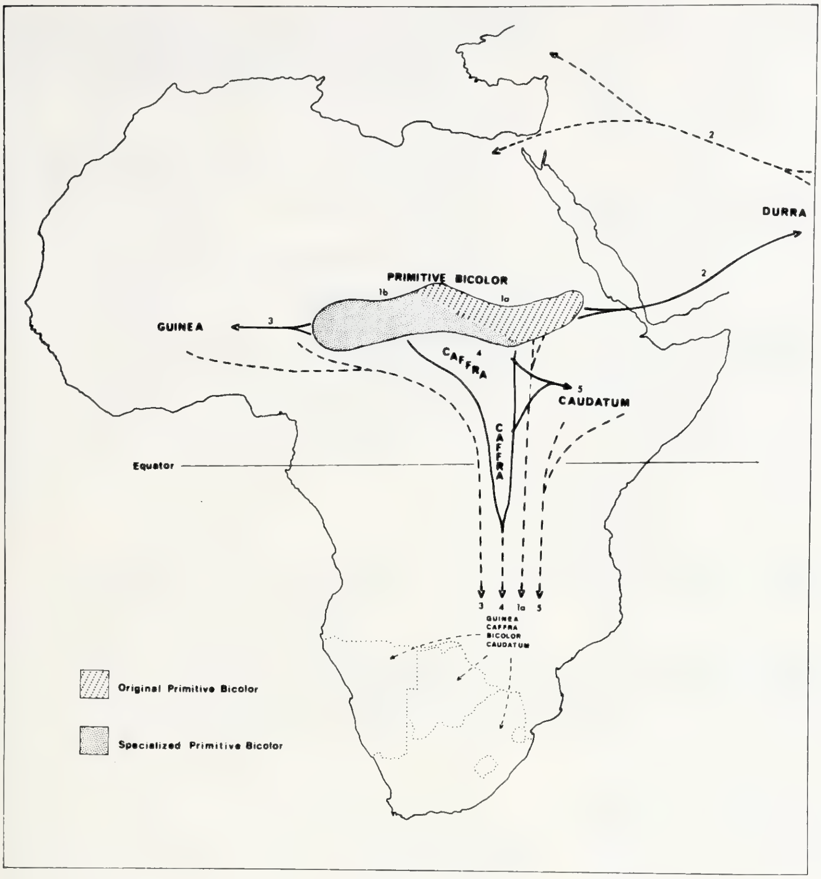

FIG. 4.—Early movement of cultivated sorghum races (adapted from Harlan & Stemler, 1976). ———→ representing movement before or during primary specialization. --------→ representing movement after primary specialization.

this race reflects an adaptation to a wet environment, and is characterized by the open, gaping glumes and turned discoid grains (Stemler *et al.*, 1975; De Wet *et al.*, 1972), as well as the upper glume having strongly inturned margins. Race Guinea is most closely related to race Bicolor. Characters shared by these two races, but absent in races Caffra, and Caudatum, include long glumes which exceed the grain in length, a primitive open inflorescence and sweet stems. The zone of weakness and basal groove are less developed in this race than in races Caffra and Caudatum.

The second line of evolution from specialized primitive Bicolor is the Caffra line, which includes races Caffra and Caudatum (Fig. 3–C2). Evolution of this line probably started sometime before the migration of cultivated sorghums southwards, with selection favouring the compacting of the inflorescence, further development of the zone of weakness, shortening of the glumes and the loss of sweet stems, due to a preference towards grain production. This specialization probably continued during the early parts of the movement of primitive Caffra southwards (Fig. 4–4), but would have been largely complete by the time the equator had been reached. Race Caffra is, therefore, not seen as having had an independent origin in the southern part of Africa, presumably from race Verticilliflora, as suggested by De Wet & Harlan (1971) and Schechter & De Wet (1972).

Race Caudatum is morphologically very similar to race Caffra, sharing with it all the specialization of the Caffra line of evolution. The distribution of present-day race Caudatum is concentrated in central and eastern Africa which, together with the morphological features shared with race Caffra, suggests that it is a derivative of race Caffra (Fig. 3–D), developed from members of this race remaining behind in central Africa after the movement of race Caffra into southern Africa (Fig. 4–5). Race Caudatum has a single derived character, the asymmetrical grain, not present in typical Caffra sorghums. All available evidence, therefore, points to race Caudatum being of recent origin, as concluded by Harlan & Stemler (1976), rather than being a relatively old race because it occupies an area of first sorghum cultivation, as proposed by De Wet *et al.* (1976).

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A preliminary survey of primitive crops cultivated in the northern Transvaal of South Africa

T. H. ARNOLD* and K. J. MUSIL*

ABSTRACT

The different tribal economies of South Africa rely extensively on a number of primitive crop taxa which are cultivated as a primary food source. The most important of these include *Sorghum bicolor, Pennisetum americanum, Citrullus lanatus, Lagenaria siceraria, Vigna unguiculata, Voandzeia subterranea* and *Hibiscus esculentus.*

Morphological variation within these and a number of less important crops is discussed. The frequency with which each crop is grown and preference ratings allotted to them by individual tribal families are compared between the three major ethnic regions of the northern Transvaal. Factors which determine preferences are also discussed and suggestions made relating to germ plasm conservation.

RÉSUMÉ

UN RELEVÉ PRÉLIMINAIRE DES CULTURES PRIMITIVES PRATIQUÉES DANS LE NORD DU TRANSVAAL EN AFRIQUE DU SUD

Les économies tribales différentes d'Afrique du Sud reposent largement sur un nombre de taxa de cultures primitives qui sont cultivées comme sources primaires d'alimentation. Les plus importantes de cel-les-ci incluent Sorghum bicolor, Pennisetum americanum, Citrullus lanatus, Lagenaria siceraria, Vigna unguiculata, Voandzeia subterranea *et* Hibiscus esculentus.

La variation morphologique existant chez celles-ci ainsi que dans un nombre de cultures moins importantes est discutée. La fréquence avec laquelle chaque culture est pratiquée et les degrés de préférence qui leur sont attribués par des famille tribales individuelles sont comparés entre les trois régions ethniques majeures du Transvaal du Nord. Les facteurs qui déterminent les préférences sont aussi discutés et des suggestions sont émises en ce qui concerne la conservation du patrimoine génétique.

INTRODUCTION

Little is known about the exact nature and diversity of primitive crop taxa cultivated in South Africa, despite that many of these crops, for example, *Sorghum bicolor, Pennisetum americanum, Vigna unguiculata* and *Citrullus lanatus,* exhibit a considerable range in variation and are extensively cultivated by the various ethnic groups throughout the country.

The majority of these crops are considered to have originated and evolved in North and West Africa (Harris, 1976), with South Africa representing merely the southern most extreme of their distibution. This may account, at least in part, for many workers (De Wet, 1972; Doku & Karikari, 1971; Stemler *et al.*, 1977 and Westphal, 1974), investigating the origin, evolution and taxonomy of these crops, having focused their attention upon the northern half of the continent. Where reference is made in the literature to primitive crops grown in this country (Brunken *et al.*, 1977; De Wet & Huckabay 1967; De Wet *et al.*, 1976; Harlan & Stemler, 1976; and Fursa, 1972), it is largely inadequate, based on limited information and usually forms part of more detailed investigations centred around the region of origin of these crops.

In order to expand our knowledge of primitive crops grown in South Africa and bring it into line with that from elsewhere in Africa, a detailed study of the morphological variation and distribution of these crops is being undertaken by the present authors, together with extensive germ plasm collection. Included in this paper is some of the information so far collected from the Transvaal, which is presented essentially as an introduction to a much wider study covering the whole country.

STUDY AREA AND SAMPLING METHODS

Information presented in this paper was gathered during a pilot study of the ethnic regions of Lebowa, Gazankulu and Venda in the northern Transvaal of South Africa (Fig. 1), and represents part of a more extensive survey to be undertaken throughout the Republic of South Africa.

A total of 119 families from 73 villages was interviewed in the three regions. These include: Lebowa — 17 families from 13 villages, Gazankulu — 67 families from 31 villages, and Venda — 35 families from 29 villages. With the help of interpreters, a questionnaire was completed for each family. Herbarium specimens and seed were collected to support the information gathered for the questionnaire.

It is impossible to provide definite conclusions as to the nature and variability of the crops cultivated, because only a limited number of families were sampled in each village. Additional information requires to be gathered for a more complete assessment of the situation.

MORPHOLOGICAL VARIATION

Eight major primitive, dryland crops, considered by Harris (1976) to be of African origin, are

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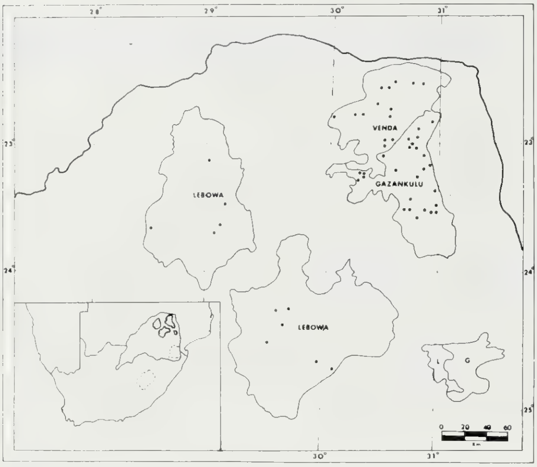

FIG. 1.—Study area. Black dots represent villages sampled. Single dots sometimes represent more than one village situated in close proximity to one another.

cultivated within the study area. These include *Sorghum bicolor* (L.) Moench, *Pennisetum americanum* (L.) K. Schum., *Vigna unguiculata* (L.) Walp., *Voandzeia subterranea* (L.) Thouars, *Citrullus lanatus* (Thunb.) Matsumura & Nakai, *Lagenaria siceraria* (Molina) Standl. and *Hibiscus esculentus* L. Important crops of extra-African origin include *Zea mays* L., *Arachis hypogaea* L., *Cucurbita* sp. (cf. *C. pepo* L.) and *Phaseolus radiatus* L.

The extent to which each crop varied morphologically differed between the taxa. *Phaseolus radiatus* and *Hibiscus esculentus* showed little variation, whereas the remainder showed extreme variation not only at the regional level but also within a single village and even within individual cultivated fields. Variation within the major primitive crops is discussed below, as well as that observed in *Arachis hypogaea* and *Cucurbita* sp.

Sorghum bicolor *(Sorghum).*

All five cultivated races of *S. bicolor* recognized by De Wet (1978) were recorded. Race Caffra is the most common, followed by races Guinea and Bicolor. Caudatum sorghums were present in Venda, with a single collection from Lebowa, and race Durra was recorded twice from a single village in Venda.

Morphological variation was considerable in all the races except race Durra, with Caffra sorghums exhibiting the greatest amount of variation. Variation within each race was expressed largely in the size and degree of compaction of the inflorescence, the number of grains per inflorescence, the colour of the glumes, and the size and colour of the grains. Seven Intermediate races were also observed (Intermediate races according to Harlan & De Wet, 1972). Morphological variation in South African sorghums is discussed in greater detail by Arnold (1982).

Pennisetum americanum *(Bulrush/Pearl millet)*

This crop is cultivated in differing amounts throughout the study area. Weedy forms (subsp. *stenostachyum*), distinguished by their disarticulating spikelets, were often found growing alongside cultivated forms (subsp. *americanum*). The amount of variation observed within this crop differed markedly between the different regions. In Lebowa variation of the inflorescence was minimal, whereas in Venda it was often difficult to find two inflorescences from a single field that looked suitably alike.

Throughout the study area inflorescence length ranged between 10 and 55 cm, and included club as well as candle-shaped forms. Involucral bristles (3–10 mm in length) varied from $\frac{2}{3}$ spikelet length in some individuals to three times spikelet length in others. Grain size also varied (2,1–4,1 mm by 1,3–2,5 mm) as did grain colour which ranged from cream-yellow to light or dark grey.

Vigna unguiculata *(Cowpea)*

Cowpeas are commonly cultivated in all three regions. Two basic forms were collected: a soft, purple-podded form characterized by purple leaves; and a hard, cream-podded form with green leaves. The beans were found to be extremely variable, particularly in colour, but also in size and shape. Colour forms included cream, beige, orange, red, mauve, purple and black and were either plain-coloured or speckled. A high proportion of diminutive, angular beans were also observed.

Voandzeia subterranea *(Juga bean/African or Bambarra groundnut)*

Juga beans exhibited similar although less variation than cowpeas. This was manifested mainly in the colour of the beans, which ranged from cream (often with black around the hilum) to beige, orange-brown, red, purple and black. Speckled forms of most of these colours also exist.

Citrullus lanatus *(Watermelon)*

Two major types are grown. The first includes the sweet melons which have a relatively spongy, sweet, cream-white or pink flesh, and are eaten raw immediately they are harvested. The second type includes the cooking melons, with an insipid tasting, slightly firmer flesh, ranging in colour from cream-white to pale yellow or salmon-orange.

Melon size ranged from 10–35 cm in length (diameter in spherical forms). Skin colour patterning is highly variable, being plain light or dark green, or cream-green coloured (cooking type) or a combination of these colours, either mottled, speckled, or arranged in stripes (sweet and cooking types). Intermediate patterns also exist. The seeds showed a similar range in variation, ranging in length from 0,9–1,4 cm and in colour from cream to green, light or dark brown, red and black. Speckled forms of the green, brown and red colours also exist.

Lagenaria siceraria *(Gourd/Calabash)*

As in the case of the watermelons, calabashes are grown throughout the study area. Variation is limited to the fruits and seeds. Two basic groups are recognized by the different ethnic tribes, based on utilization. In the first group, the calabashes are characterized by their suitability for use as household utensils (water or medicine containers, bowls, scoops for water, beer or meal, etc). Calabashes that cannot be used as utensils comprise the second group cultivated specifically for eating.

A number of basic fruit shapes can be recognized in both the utensil and eating forms, but at this stage these have not been formally categorized. Intermediate shapes have also been collected. The colour of the skin remains relatively uniform, varying between light and dark green and changing with age to cream-beige. Skin texture is either smooth or rough (covered in small ± 1 cm high rounded or angled growths). The rough forms are always eaten irrespective of their shape.

The seeds comprise two major types, those with wing-like margins and those without. A single intermediate form with the margins partly developed has been observed. Seeds range in size from 1,3–2,5 cm in length and 0,9–1,4 cm in width and vary in colour to include cream-yellow, brown and olive-brown.

Hibiscus esculentus *(Okra)*

Together with *Sesamum indicum,* this crop is grown almost exclusively in Gazankulu (by 60% of the families interviewed) and in immediately adjoining areas of Lebowa and Venda. This suggests a later introduction into South Africa than other primitive crops, possibly from Moçambique. Two forms are recognized by the families who grow this crop: the first includes plants with short, fat fruits 7,8–10,0 cm long and 3,6–3,8 cm broad, whereas those of the second form are noticeably long and thin, 11,4–13,8 cm long and 2,1–2,2 cm broad. A range of intermediates exists between these two extremes.

Phaseolus radiatus *(Mung bean)*

Although grown in Gazankulu and Venda, mung beans are important only in Lebowa where they are grown by 53% of the families interviewed. Morphological variation in the three regions is minimal. Throughout the study area this crop was erroneously referred to as China pea by the villagers. According to Westphal (1974), China pea is one of the many common names for *Vigna unguiculata.*

Arachis hypogaea *(Peanuts/Groundnuts)*

This species is not native to Africa and is probably a recent introduction into tribal agriculture in South Africa. Peanuts are grown in varying amounts throughout the study area. Three distinct forms are cultivated differing in the size and colour of the nuts. These include a long red form (1,7–2,3 cm by 0,8–1,1 cm), a small dark red form (0,9–1,4 cm by 0,6–0,9 cm) and an intermediate pink form (1,1–1,7 by 0,7–1,0 cm).

Cucurbita *sp. cf.* C. pepo *(Pumpkin/Squash)*

Like *Arachis hypogaea,* this crop is not native to Africa. It is considered to be a relatively recent introduction into tribal agriculture, possibly a derivative of one or more of the modern pumpkin or Hubbard squash forms grown throughout the country. Pumpkins are an extremely important crop, not only because they are grown throughout the study area, but also because selection has produced forms that are extremely hardy and reasonably well adapted to survive under low rainfall, dryland agricultural conditions. It is impossible at this stage to give a realistic assessment of the variation exhibited by this crop.

Minor crops

Crops of minor importance that are also grown include: *Saccharum* sp. (sugar cane); *Eleusine coracana* (L.) Gaerth (finger millet); *Cajanus cajan* (L.) Millsp. (pigeon pea); *Phaseolus acutifolius* Gray var. *latifolius* Freem. (tepary bean); *Mucuna* sp. (velvet bean); *Ipomaea batatas* (L.) Lam. (sweet potato); *Manihot esculenta* Crantz (cassava); *Sesamum inducum* L. (sesame); *Ricinus communis* L. (castor-oil bean). The variation exhibited by these crops was either negligable or not sufficiently well recorded to be discussed in this paper.

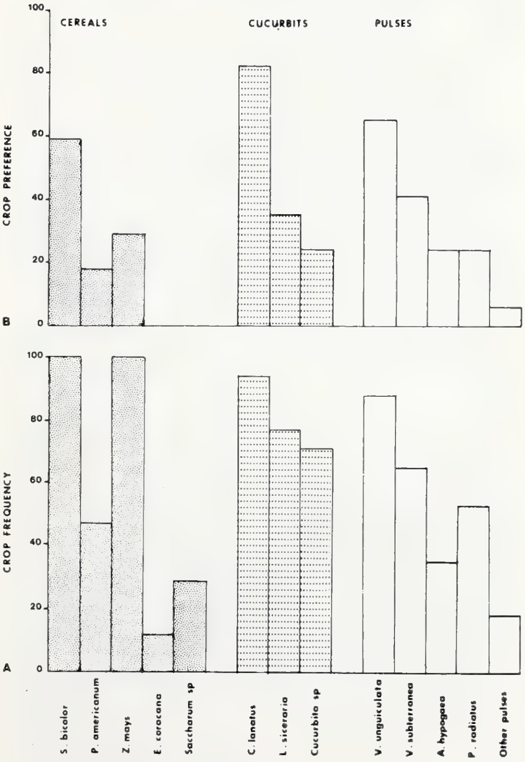

FIG. 2.—Relative frequencies and preference ratings of major crops cultivated in Lebowa.

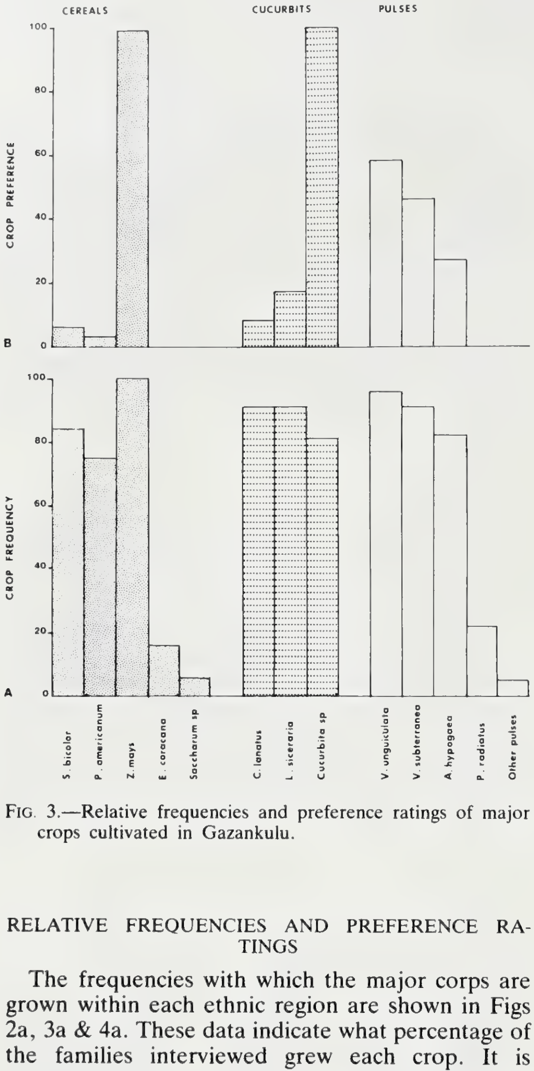

FIG. 3.—Relative frequencies and preference ratings of major crops cultivated in Gazankulu.

RELATIVE FREQUENCIES AND PREFERENCE RATINGS

The frequencies with which the major corps are grown within each ethnic region are shown in Figs 2a, 3a & 4a. These data indicate what percentage of the families interviewed grew each crop. It is important to note that frequency represents merely whether the crop was or was not cultivated by individual families and not the extent (area under cultivation) to which it was grown.

At this stage of the survey, frequency is considered to be a better indicator than abundance on which to base germ plasm conservation priorities.

In Lebowa 65% of the families interviewed grew seven of the ten major crops available, with at least two crops from each of the differenct crop groups (cereals, cucurbits and pulses), including the three extra-African taxa, being represented. In Gazankulu 74% of the families grew all the major crops in varying amounts, whereas in Venda 66% of the families grew eight of the ten most important crops.

This tendency to grow as many of the major crops as possible irrespective of whether climatic conditions favour their growth may be ascribed to a need to safe-guard against periods of climatic extremes. The drier parts of the study area are particularly prone to periods of drought which seriously affect the cultivation of maize, sorghum (in some areas), pumpkins and peanuts. When these crops are favoured in such areas the more drought resistant taxa are also planted, but to a lesser extent, thus ensuring at least some food during bad years. Another reason for planting a large variety of crops is that besides providing a varied diet, they also provide a variety of foods with differing tastes. Also significant is that many crops have a particular desirable quality absent in other similar crops, for example, although maize is preferred in Gazankulu for meal, limited amounts of sorghum and *Pennisetum americanum* are also grown for making beer. Similarly, although *Lagenaria siceraria* is a relatively low priority crop throughout the study area, it is still cultivated, being the only crop from which household utensils are made.

Preference indicates the relative importance attached to each crop by different ethnic tribes and is seen also as a potential indicator of possible trends towards or away from specific crops. The data presented in Figs 2b, 3b & 4b represents the percentage of families that allotted a 1st preference rating to the various crops. As some families gave a priority one rating to more than one crop, the percentage totals for the different crop groups (cereals, cucurbits and pulses) generally exceeded 100%. Preferences did not necessarily reflect the frequency with which the different crops were grown. Where preferences contrasted strongly with frequencies, this was due largely to the tendency for the majority of families to grow as many of the major crops as possible. The reasons for this have already been discussed.

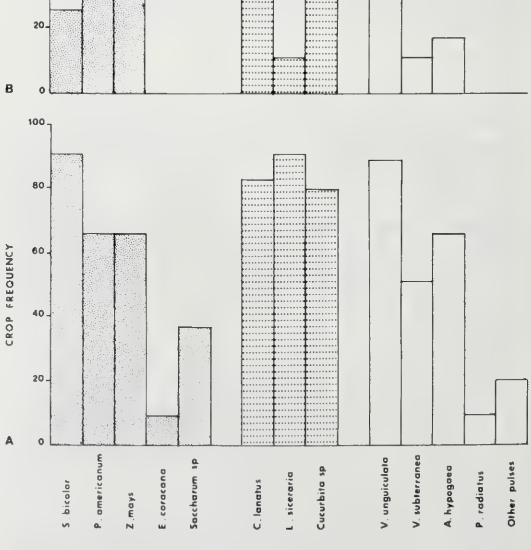

FIG. 4.—Relative frequencies and preference ratings of major crops cultivated in Venda.

Cereals

In Lebowa (Fig. 2) *Pennisetum americanum* is less frequently grown (47% of the families) than sorghum and maize (100% respectively). This is also shown by the preference ratings. Although *P. americanum* is more suited to the drier parts of this region, sorghum is more frequently grown as it is considered much more palatable. In Gazankulu (Fig. 3), maize constitutes a serious threat to sorghum and *P. americanum* cultivation. It is grown in large quantities throughout the region and is preferred by the vast majority of families. The cultivation of cereals in Venda (Fig. 4) is closely related to the climate of the region and is also closely correlated with the preference rating for each of these three crops.

Cucurbits

In Lebowa (Fig. 2) the frequency of these crops follows the trend of preference ratings alloted to them. In Gazankulu (Fig. 3) pumpkins are highly preferred to watermelons and gourds despite all three of these crops being grown by 80% of the families. In Venda (Fig. 4) the three cucurbits were grown with similar frequency. The reason for the low preference rating for *Lagenaria siceraria* throughout the study area is due, at least in part, to the increasing supply of metal and plastic utensils from local stores.

Pulses

Vigna unguiculata, grown by 88% of the families in Lebowa, is the most important pulse crop in this region (Fig. 2). Here, unlike Gazankulu and Venda, *Phaseolus radiatus* is also commonly cultivated (53% of the families). This latter crop, although occasionally eaten, is grown mainly as a cash crop. The frequency of pulses grown in Gazankulu (Fig. 3) follows closely the preference ratings allocated to these crops. A similar situation was also found in Venda (Fig. 4), with the exception of *Voandzeia subterranea* which is both less preferred and less grown than in Gazankulu and Lebowa, being considered a less versatile crop than *Vigna unguiculata* and lower yielding than *Arachis hypogaea.*

FACTORS DETERMINING PREFERENCES

Whether a crop is cultivated or not and the extent to which it is cultivated, is determined largely by individual preferences (see Figs 2b, 3b & 4b). Preferences, in turn, are determined by a number of factors, working individually or more commonly in combination.

Diversity of Use

In Gazankulu maize is preferred to sorghum and pearl millet because, besides providing meal for porridge, it can also be eaten as a green vegetable during the growing season. Throughout the entire study area, and particularly in Venda, *Vigna unguiculata* is preferred to other pulses because, not only can the beans be eaten green, or dried and stored for later consumption, but the leaves can be eaten as spinach. Similarly, pumpkins not only have edible fruits, but the leaves can be prepared as a vegetable and the male flowers dried and stored for later consumption.

Long-term storage

Crops which can be stored are preferred to those which cannot. Cooking forms of *Citrullus lanatus* and pumpkins are therefore generally preferred to edible forms of *Lagenaria siceraria.*

Resistance to insect attack

The small seeds of pearl millet are less susceptible to insect attack during storage than most other cereals. This crop is therefore favoured more than sorghum and maize in southern Lobowa, west Venda and north-west Gazankulu.

Palatability

In the low rainfall areas of Lebowa *Pennisetum americanum* is considered highly unpalatable and is replaced by sorghum.

Relative yields

Preferences favour high yielding crops. Yield is generally closely related to annual rainfall and to soil type. In Venda (Fig. 5.1) pearl millet, although grown over a wide range of rainfall, is preferred to sorghum and maize in areas with an annual rainfall between 400 and 460 mm. As the annual rainfall increases from 460 to 520 mm, sorghum yields increase and surpass those of pearl millet. In these areas sorghum is preferred. Where the annual rainfall exceeds 520 mm, maize is generally higher yielding than sorghum or pearl millet and is therefore preferred to both these crops.

Although similar, the situation in Lebowa (Fig. 5.2) is complicated because *Pennisetum americanum* is considered unpalatable in areas of low rainfall (400–480 mm). It is consequently replaced by the relatively lower yielding sorghum in these areas.

In Gazankulu (Fig. 5.3) the annual rainfall is between 520 mm and 760 mm for the villages sampled. Within this range, pearl millet and sorghum yield less than maize and are therefore not preferred. Where preferences were recorded for these two crops, they were shared equally with maize.

Soil type

It was generally observed for the cereals that the range in rainfall under which the respective crops grew best was increased or reduced depending on the nature of the soils. Well drained, sandy soils extend the upper rainfall limits at which sorghum and pearl millet are preferred, while reducing preference limits for maize. On the other hand, soils that tend to retain moisture extend the lower preference limits of sorghum and maize.

Commercial value

In Lebowa *Vigna unguiculata,* and in particularly the large speckled blue-grey seeded form which can be sold to the local milling company in Pietersburg

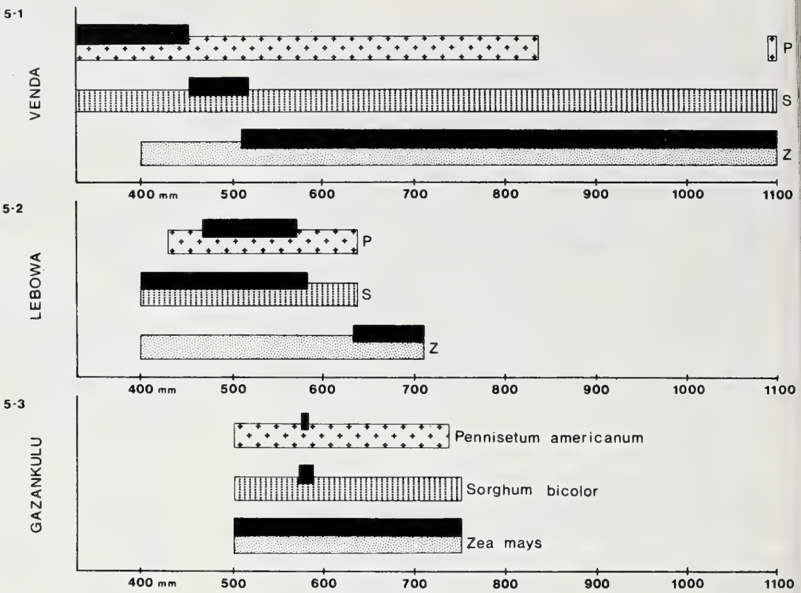

FIG. 5.—Relationship between annual rainfall and cereals cultivated in the three regions of the study area. Black bands represent range in annual rainfall over which the individual crops were given a priority one rating.

for cash, is preferred to most other pulses. Similarly *Phaseolus radiatus* is grown almost exclusively as a cash crop in this region, and is therefore more frequently grown and preferred than in Gazankulu or Venda.

Susceptibility to bird damage

In many parts of the study area birds are a major problem, destroying large fields of sorghum and in particular *Pennisetum americanum.* In north-east Lebowa, south Venda and north-east and south Gazankulu the problem is so great that *P. americanum* is largely excluded from cultivation.

Nutritional value

In parts of Lebowa where sorghum is preferred it is believed that this crop prevents infantile-pellagra (caused by a protein deficiency), while maize does not. Consequently, sorghum is preferred to maize.

GERM PLASM CONSERVATION

One of the primary aims underlying this survey, besides being to assess the nature and variation of primitive South African crops, is the collection and preservation of germ plasm and the assignment of conservation priorities to these crops.

Most of the major primitive crops show a wide range in morphological variation and accordingly constitute a valuable source of germ plasm. Efforts to collect and preserve this germ plasm have been minimal in the past, largely due to a lack of realization as to its potential value. As a result manpower and funding allocated to this work has been limited. This fact is reflected in the mere 201 collections of primitive crops housed in the national seed bank (Department Agriculture and Fisheries, 1980). Included in this total are: *Sorghum bicolor* 118, *Pennisetum americanum* 27, *Eleusine coracana* 1, *Citrullus lanatus* 15, *Lagenaria siceraria* 3, *Vigna unguiculata* 19, *Voandzeia subterranea* 15, *Phaseolus radiatus* 0, *P. acutifolius* 0, *Cajanus cajan* 0, *Sesamum indicum* 1 and *Ricinus communis* 2.

Poor collecting is not the only problem facing the conservation of primitive crop germ plasm in South Africa. In many parts of the study area there is an increasing tendency to move away from low yielding primative crops, and to replace these with better developed higher yielding modern crop types. This is particularly noticeable with cereals, where maize cultivation is being strongly promoted by all local agricultural authorities. This trend is also seen in the increasing importance of *Cucurbita* sp. cf *pepo* and *Arachis hypogaea* as agricultural crops. These changes are particularly, although not exclusively, prevalent in areas where irrigation has been made available. In these situations, the cultivation of vegetables (onions, tomatoes, chillies, cabbages and various bean types, etc), as well as fruit crops (pawpaws, oranges, mangoes, bananas, avocados and guavas) is also promoted, all of which influence the extent to which primitive crops are cultivated. Such changes in attitude do not necessarily mean that the cultivation of primitive crops is being discontinued. In most situations it is merely the reduced area cultivated (up to 90%) that causes a serious loss in germ plasm.

In assessing the situation in South Africa, it is apparent that a concerted effort is required to collect germ plasm of all primitive crops, and that this should include as much as possible of the variation expressed by these crops. In addition, the need to prescribe special conservation priority ratings to certain crops within the ethnic regions studied has emerged from this survey. Special consideration should be given to all minor crops through the study area as well as to *Pennisetum americanum* in the low rainfall areas of Lebowa, to *Sorghum bicolor* and *Pennisetum americanum* in Gazankulu and to *Voandzeia subterranea* in Venda.

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Santé et valorisation des plantes médicinales en Côte d'Ivoire

L. AKÉ ASSI*

RÉSUMÉ

Les plantes médicinales sont les diverses espèces végétales dont les différentes parties sont utilisées empiriquement pour combattre les affections, endémiques ou non, dont souffrent nos régions.

La Côte d'Ivoire, comme la plupart des pays tropicaux, possède une flore abondante, riche en espèces dont certaines, contenant des principes actifs, permettent de préparer des remèdes servant au traitement de nombreuses maladies.

En effet, l'art de guérir toutes les maladies est exercé à l'état empirique par des guérisseurs, résidant dans toutes les régions de la Côte d'Ivoire.

En zone rurale, chaque habitant connaît et utilise les vertus d'une ou plusieurs plantes.

En Afrique noire en général, la médecine traditionnelle assure de 80 à 90 % de la couverture sanitaire de la population. Elle a l'avantage d'être plus à la portée de la main, et permet de se soigner à moindres frais.

C'est pourquoi, il serait souhaitable que cette médecine reçoive toute l'attention à laquelle elle a droit, pour plusieurs raisons.

L'étude des plantes médicinales permettra de fabriquer, sur place, des médicaments à base de matières premières locales. Ce projet favorisera, outre la promotion des ressources du pays, des possibilités d'emplois.

Dans le cadre de l'Ethnobotanique, les enquêtes menées auprès des guérisseurs dans quelques régions de la Côte d'Ivoire, ont permis le recensement de plusieurs recettes médicamenteuses qui ont fait l'objet de plusieurs rapports ou publications.

Pourtant, le recensement, encore insignifiant en matière de végétaux utiles pour la santé humaine, limite considérablement les possibilités de la phytothérapie. Un nombre important de plantes reste encore à étudier et à valoriser.

Malheureusement, la destruction inconsidérée et accélérée, en de multiples régions du pays, des espaces naturels, rend chaque jour plus difficile la découverte ou l'exploitation rationnelle des potentialités de nos ressources végetales.

C'est pourquoi, avant qu'il ne soit trop tard, il serait indispensable que le recensement entrepris pour cataloguer les plantes médicinales puisse être intensifié et élargi à l'échelon national, voire interafricain.

A ce sujet, il serait nécessaire d'inciter les gouvernements africains à prendre des mesures draconiennes pour sauver notre patrimoine médicinal en peril.

ABSTRACT

HEALTH AND THE EVALUATION OF MEDICINAL PLANTS IN THE IVORY COAST

The Ivory Coast, like most tropical countries, has a rich flora with many species, some of which contain active principles used in the preparation of useful remedies for the treatment of disease.

The art of curing disease is practised in a very empirical way by healers all over the Ivory Coast.

In intertropical Africa, generally speaking, traditional medicine accounts for about 80–90% of the medicinal needs of the population. It has the advantage of being near at hand and provides medical treatment at low cost.

The study of medicinal plants will result in the production locally of medicines from indigenous raw materials, and the project, in addition to the exploitation of national resources, will create work opportunities.

Concerning ethnobotany, investigations carried out among healers in some areas of the Ivory Coast, have enabled the registration of several medicinal recipes that have resulted in various reports and publications.

Yet, slow progress with the registration of plants of use in human health restricts the possibilities of phytotherapy. Clearly, many plants remain to be studied and evaluated.

Unfortunately, thoughtless and rapid destruction of natural areas in several parts of the country, makes the discovery and judicious exploitation of our plant resources increasingly difficult.

Therefore, it is necessary to urge African governments to take draconian actions in order to save our endangered medical heritage.

Les plantes médicinales sont les diverses espèces végétales dont les différentes parties sont utilisées empiriquement pour combattre les affections, endémiques ou non, dont souffrent nos régions.

La Côte d'Ivoire, comme la plupart des pays tropicaux, possède une flore abondante, riche en espèces.

Environ 1/3 des représentants ivoiriens de la flore phanérogamique ainsi qu'une infime minorité de Thallophytes (Lichens et Champignons supérieurs) offrent un grand choix de plantes à principes actifs, dont les propriétés curatives ou toxiques permettent la préparation de remèdes servant au traitement de nombreuses maladies dans toutes les contrées du pays.

Car il est difficile à croire que c'est uniquement par la sélection naturelle et sans aucun moyen

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thérapeutique que nos populations ont survecu aux vicissitudes du temps et à toutes les maladies dont certaines sont encore endémiques aujourd'hui.

En effet, l'art de guérir pratiquement toutes les maladies est exercé à l'état empirique par des guérisseurs de grande renommée, résidant dans toutes les régions de la Côte d'Ivoire.

La connaissance ancestrale qu'ont les populations des plantes médicinales de leur environnement est la médecine traditionnelle. Cette connaissance est transmise et perfectionnée de génération en génération par la tradition orale, généralement à des initiés appelés 'guérisseurs', ou 'tradipraticiens' en terme moderne.

En zone rurale, chaque habitant connaît et utilise les vertus d'une ou plusieurs plantes.

Les guérisseurs, plus éclairés que les autres, examinent, posent le diagnostic des maladies. Ils récoltent les plantes, préparent et administrent les médicaments. On les rencontre dans tous les milieux, aussi bien dans les villages que dans les villes.

Leurs activités thérapeutiques sont habituellement secondaires, car ils sont d'abord agriculteurs, artisans ou même employés. Les guérisseurs (hommes ou femmes) sont, soit généralistes, soit spécialistes.

En Afrique noire au sud du Sahara en général, cette médecine assure de 80 à 90 % de la couverture sanitaire des populations.

En effet, les prix de revient élevés des médicaments préparés dans les pays industrialisés sont un frein à leur emploi dans la plupart des pays en voie de développement.

Environ 10 à 20 % seulement de la population bénéficient des soins médicaux modernes. Les autres, pour des raisons d'ordre économique, préfèrent recourir à la pratique traditionnelle, puiser dans le droguier local.

La médecine traditionnelle présente l'avantage d'être beaucoup plus à la portée de la main, et permet de se soigner à moindres frais, souvent même sans frais.

Pour les pays en développement en général et pour les Africains en particulier, il s'agit d'orienter notre politique sanitaire essentiellement vers la solution des besoins élémentaires de la population.

C'est pourquoi, il serait souhaitable que la médecine traditionnelle reçoive toute l'attention à laquelle elle a droit pour plusieurs raisons. C'est un héritage culturel dont toutes les richesses ne sont certainement pas encore connues. C'est un terrain peu exploré, dont toutes les possibilités doivent être examinées dans l'intérêt de la science médicale et pour le bien-être de sa population.

Le désir d'actualiser cette science du guérisseur afin de mieux la connaître a fait apparaître à tous les niveaux la nécessité de disposer sinon d'un manuel scientifique, du moins d'un catalogue aussi complet que possible.

L'étude des plantes médicinales permettra de fabriquer sur place, à base de matières premières locales, des médicaments aussi valables que les spécialités importées. Ce projet permettra, outre la promotion des ressources locales, des possibilités d'emplois.

C'est dans ce but qu'à été mise en place, depuis 1973, par le Ministère de la Recherche Scientifique, une équipe pluridisciplinaire ayant pour thème de recherche: 'Substances Naturelles à usage Pharmaceutique et Cosmétique de Côte d'Ivoire'. Des botanistes, chimistes, pharmaciens, physiologistes et physiciens collaborent à la réalisation des trois grandes opérations que comporte ce programme d'études: Ethnobotanique, Phytochimie, Physiologie.

Dans le cadre de l'Ethnobotanique, les enquêtes menées auprès des guérisseurs dans quelques localités du pays ont permis le recensement de plusieurs centaines de recettes médicamenteuses qui ont fait l'objet de plusieurs rapports ou publications. Voir bibliographie.

Quant au terme de plantes médicinales, il reste assez ambigu. Sous cette appellation, on englobe en effet, d'une part, des plantes ou des organes de végétaux qu'on emploie en nature, par exemple des feuilles de faux Kinkeliba *(Cassia occidentalis)*, de Citronnelle *(Cymbopogon citratus)*, etc., utilisées sous forme de tisane, ou des plantes servant telles quelles à des préparations d'antisporiques *(Icacina mannii, Physalis angulata . .)* ou de vulnéraires *(Baphia nitida, Cyathula prostrata, Enantia polycarpa . .)*, etc.

On voit que le domaine des plantes médicinales est fort vaste.

Le mouvement écologique et la tendance diffuse au 'retour à la nature' qu'il a engendrée rendent actuellement aux plantes médicinales un regain de faveur, parallèlement à une réserve croissante à l'égard des produits pharmaceutiques. Critiqués du point de vue de leur efficacité et de leur multiplicité, voire du point de vue de leur existence même, remis en cause pour des raisons économiques, les médicaments souffrent actuellement d'un discrédit qui n'est que la rançon des abus.

De nombreuses recherches en phytothérapie ont été effectuées ces dernières années, qui ont permis à la thérapeutique de sortir de l'empirisme. Il ne convient certes pas de sous-estimer l'oeuvre de nos anciens, qui, à partir d'observations populaires, ont dégagé les propriétés thérapeutiques de nombreux simples. Mais il était nécessaire, pour faire accéder la phytothérapie au plan scientifique, de la dégager de toute notion mystique, et de soumettre les médicaments végétaux aux critères de la recherche et de l'expérimentation modernes.

Un grand nombre de médicaments vendus en pharmacie sont d'origine végétale. La tendance s'accentue. Selon des statistiques françaises et américaines, 40 % des spécialités pharmaceutiques actuelles dérivent de végétaux et, dans la seule pharmacopée française, l'on compte plus de 8 000 plantes ou principes actifs d'origine végétale dont les pays africains sont les premiers fournisseurs.

Pourtant, le recensement encore insignifiant en matière de végétaux utiles pour la santé humaine limite considérablement les possibilités de la phytothérapie. Un nombre important de plantes africaines reste encore à étudier et à valoriser.

Malheureusement, la destruction inconsidérée et accélérée, en de multiples régions du pays, des espaces naturels rend chaque jour plus difficile la découverte ou l'exploitation rationnelle des potentialités de nos ressources végétales.

C'est pourquoi, avant qu'il ne soit trop tard, il serait indispensable que le recensement entrepris pour cataloguer les plantes médicinales puisse être intensifié et élargi à l'échelon national, voire interafricain.

A cet égard, il serait nécessaire d'inciter les gouvernements africains à prendre des mesures draconiennes pour sauver notre patrimoine médicinal en péril. Ceci, dans l'intérêt de la science de demain, pour l'humanité et pour assurer le maintien d'une bonne santé.

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Contribution a l'ethnobotanique des Warega (Maniema, Kivu, Zaïre)

M. KITEMBO*

RÉSUMÉ

Eu égard à la position sociale particulière occupée par le grand-père et une tante de l'auteur, une information fort détaillée a pu être rassemblée sur l'usage traditionnel des plantes au Maniema.

Tous les renseignements obtenus sont supportés par un herbier de référence déposé à l'Herbarium de l'Université de Lubumbashi (LSHI), ainsi que par un ou plusieurs noms vernaculaires.

Les informations sont regroupées en quatre types d'utilisation principaux, à savoir: plantes alimentaires (graines et amandes oléagineuses, fruits et graines amylacées, fleurs, organes de réserves, feuilles, fruits charnus); plantes médicinales (maladies parasitaires, gynécologie, obstétrique, etc.); plantes d'usage domestique (outils, nattes, textiles, teintures, et autres utilisations).

ABSTRACT

CONTRIBUTION TO THE ETHNOBOTANY OF THE WAREGA (MANIEMA, KIVU, ZAÏRE)

As a result of the particular social positions held by the grandfather and aunt of the author, very detailed information about the traditional uses of plants in Maniema could be collected.

All the information obtained is supported by a herbarium reference collection deposited in the Herbarium of the University of Lubumbashi (LSHI), together with one or several vernacular names.

The information can be grouped on the basis of four main types of utilization, namely plants used as food (seeds and oleaginous nuts, amylaceous fruits and flowers, leaves, berries.); medicinal plants (parasitic diseases, gynaecology, obstetrics, etc.); plants for domestic use (tools, mats, textiles, dyes and other uses).

INTRODUCTION

Le territoire occupé par les Warega est situé à l'est du Zaïre, dans la Région (= Province) du Kivu. Il est compris entre 26° et 28 40′ de longitude E et 2° et 5° de latitude S (Fig. 1). Ce territoire comprend plusieurs zones (unités administratives), à savoir: Pangi, Shabunda et Mwenga. La première de ces relève de la sous-région du Maniema, les deux dernières zones de celle du Sud Kivu La flore de ce territoire est mal connue, comme l'indique la carte du degré d'exploration botanique établie par Hepper (1979) et qui considère le Maniema comme une région mal connue. Il convient toutefois de citer les récoltes effectuées par. A. Léonard, Michelson, Delevoy, Lebrun et Pierlot (Bamps, 1968).

Des descriptions brèves de la végétation ont été réalisées par quelques botanistes et forestiers, principalement à l'occasion de traversées rapides de notre dition. Ainsi Delevoy (1928) signale que 'la forêt du Maniema est formée d'un mélange intime d'arbres de tous âges. Les arbres sont en général élancés, atteignant 15 à 25 mètres du fût, 20 à 35 mètres de hauteur totale, avec un diamètre dépassant parfois deux mètres. Dans les parties plus ou moins marécageuses, la présence de palmiers donne un caractère particulier au peuplement qui paraît moins dense'. De même Cornet (1955), qui décrit longuement l'histoire du Maniema, au travers des récits de premiers européens, reste totalement muet sur l'environnement du Maniema.

Après avoir brièvement esquissé le milieu, nous donnerons un premier inventaire ethnobotanique des Warega.

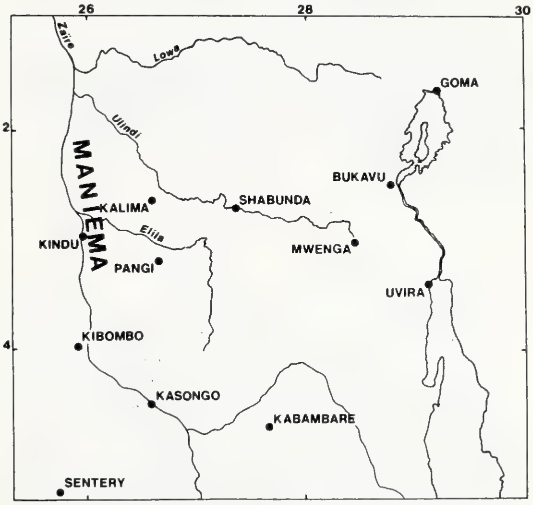

FIG. 1.—Carte de situation du Maniema.

LE MILIEU

Le Maniema est soumis à un climat équatorial de type Aw2, selon la classification de Köppen. Kindu (25° 55′ long. E, 2° 57′ lat. S., alt. 475 m) reçoit 1 637 mm de précipitations moyennes annuelles et possède une température moyenne annuelle de 25,3 °C (voir Fig. 2.). L'humidité relative moyenne y est de 79%, l'insolation annuelle moyenne de 19.301,8 dixiè-mes d'heures; elle est maximale en mai (190,6 h) et minimale en décembre (139,6 heures). Kalima situé à 900 mètres d'altitude, reçoit davantage de précipitations, soit 1917 mm en moyenne par an. C'est une région fondamentalement forestière; la forêt dense équatoriale de terre ferme est la formation végétale essentielle. Les grandes rivières,

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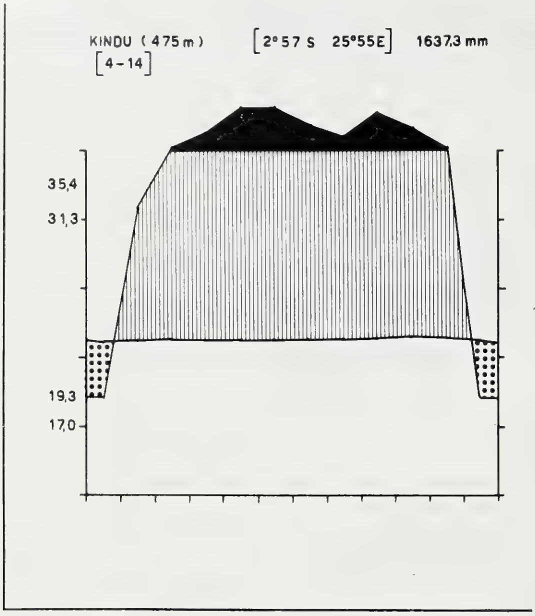

FIG. 2.—Diagramme ombrothermique de Kindu selon la technique de Walter et Lieth. La station est située dans l'hémisphère S. Le graphique débute en conséquence avec le mois de juillet.

telles que l'Elila, l'Ulindi, sont bordées de forêts galeries puissantes. Des forêts secondaires à parasoliers s'observent à proximité des villages. Ces derniers abritent une flore rudérale relativement riche.

MATERIEL ET METHODE

Matériel

Toutes les plantes signalées dans la présente note sont authentifiées par un herbier. La collection de référence (récolteur Kitembo M.) est déposée dans l'Herbarium du Laboratoire de Botanique et d'Ecologie de l'Université de Lubumbashi, dont le sigle international est LSHI (Holmgren & Keuken 1974). Un double figure au Jardin botanique national de Belgique à Meise-lez-Bruxelles (BR). Le tableau 1 reprend la liste des plantes inventoriées, le numéro de l'herbier de référence, le nom vernaculaire en dialecte lega et le type de végétation correspondant.

Méthode

Les informations ont été rassemblées par enquête directe, menée sur le terrain, en dialecte lega, au cours de deux missions respectivement en décembre 1978 et en janvier-février 1981.

OBSERVATIONS

1. *Plantes médicinales*

Maladies des enfants

Coqueluche et toux. La coqueluche ou la toux chez les enfants sont soignées par absorption d'une infusion de feuilles de *Scleria barteri.*

Diarrhée et dysenterie. Ces affections sont combattues, chez les enfants, par la consommation d'une bouillie de grains de riz grillés et pilés, soit en buvant de l'eau où a macéré de l'écorce de *Rauvolfia congolana*, soit encore par un lavement avec la décoction de feuilles d'*Achyranthes aspera.*

Constipation. La constipation est traitée par lavement avec la décoction de feuilles de *Chenopodium ambrosioides.*

Rougeole. La rougeole est traitée par lavement avec les décoctions de feuilles de *Harungana madagascariensis* et de *Solanum incanum.*

Convulsion. Pour réveiller un enfant en convulsion, on lui fait respirer, jusqu'à ce qu'il tousse, des feuilles écrasées d'*Acalypha.*

Favoriser la marche précoce du bébé. La marche du bébé de moins d'un an est favorisée par les lavements avec la décoction d'*Oldenlandia corymbosa.*

Maux de têtes

Les maux de têtes sont soignés de différentes façons. On utilise l'instillation dans les yeux du jus de feuilles écrasées de *Pauridiantha dewevrei.*On peut encore frotter le front avec les fruits des palmiers *Elaeis.* On traite encore les maux de têtes par de petites entailles au front, suivies de frottements avec la cendre des tiges de patates douces (*Ipomoea batatas*).

Conjonctivite

La conjonctivite est soignée en écrasant certaines feuilles et en les instillant dans les yeux. Nous avons connaissance de l'usage des feuilles de *Phyllanthus muellerianus*, de tomate et de *Trema orientalis.*

Diarrhée et dysenterie

La diarrhée et la dysenterie sont soignées par l'ingestion de cendres, d'eau de macération ou d'infusions. Les cendres de *Phyllanthus muellerianus* sont mélangées à celles de *Harungana madagascariensis* et on y ajoute un peu de sel; ce mélange est consommé. On utilise encore les cendres de *Musanga cecropioides.* Pour les boissons, elles sont préparées à partir de l'eau de macération des écorces de *Rauvolfia congolana* ou de l'infusion des feuilles de *Pauridiantha collicarpoides.*

Constipation et ballonnement du ventre

Ces affections sont traitées soit par lavement avec la décoction de *Chenopodium ambrosioides*, soit en buvant la sève obtenue après incision de la racine du *Musanga* ou la décoction de *Thomandersia congolana.*

Hépatite

L'hépatite se soigne par des boissons et des lavements. Pour les boissons, on utilise la décoction de *Sida rhombifolia* et l'infusion de l'écorce de *Rauvolfia congolana.* Les lavements sont effectués avec la décoction de *Smilax kraussiana*, de *Spermacoce latifolia*, de *Lycopodium cernuum* et de *Solanum incanum*, ainsi qu'avec les infusions de *Phyllanthus muellerianus* et de *Harungana madagascariensis.*

TABLEAU 1.—Principales plantes médicinales du Maniema

	No herbier de référence (1)	Nom vernaculaire (dialecte lega)	Type de végétation
PTERIDOPHYTES			
Lycopodiaceae			
Lycopodium cernuum L.	K.M. 31	Ndelelele	Vég. pionnière
Schizeaceae			
Lygodium microphyllum (Cav.) R. Br.	K.M. 56	Mwende za minkomba	Forêt galerie
Selaginellaceae			
Selaginella sp.	K.M. 42	Lwanzo lwa mbwa	Forêt galerie
ANGIOSPERMES			
Acanthaceae			
Thomandersia congolana De Wild. et Th. Dur.	K.M. 65	Mabesebese	Forêt dense sèche
Amaranthaceae			
Achyranthes aspera L. var. *aspera*	K.M. 28	Lukolokosi	Pionnière de jachêre
Apocynaceae			
Rauvolfia congolana De Wild. et Th. Dur.	K.M. 52	Kantonko	Forêt secondaire
Tabernanthe iboga Baillon	K.M. 50	—	Forêt dense sèche
Arecaceae			
Calamus deerratus Mann.	K.M. 60	Lububi	Forêt marécageuse
Asteraceae			
Bidens pilosa L.	K.M. 69	Katotoka	Rudérale
Sonchus sp.	K.M. 48	Kagili	Messicole de rizière
Caesalpiniaceae			
Gilbertiodendron dewevrei J. Léonard	K.M. 39	—	Pionnière de jachère
Chenopodiaceae			
Chenopodium ambrosioides L.	K.M. 33	Nyasunda	Rudérale
Commelinaceae			
Palisota ambigua C.B.Cl.	K.M. 26	Kimokomoko	Marécageuse
Palisota aff. P. *pynaertii* De Wild.	K.M. 24	Lukusa	Forêt galerie
Cyperaceae			
Scleria barteri Boeck.	K.M. 47	Kasalaguzi	Forêt secondaire
Euphorbiaceae			
Acalypha sp.	K.M. 7	Nyenyenkulu	Rudérale
Alchornea hirtella Benth.	K.M. 16	Bunzokanzoka	Forêt galerie
Phyllanthus muellerianus (Kuntze) Exell	K.M. 51	Ikoko lya nkulu	Forêt galerie
Fabaceae			
Desmodium hirtum Guill. et Perr.	K.M. 40	Kalema ka basombo	Endroits sablonnex
Tephrosia sp.	K.M. 62	Kabaka	Plante cultivée
Guttiferae			
Harungana madagascariensis Poir.	K.M. 37	Muntungulu	Forêt secondaire
Leeaceae			
Leea guineensis G. Don	K.M. 13	Ibilabondo	Forêt secondaire
Liliaceae			
Smilax kraussiana Meissn.	K.M. 4	Musolesole	Forêt secondaire
Malvaceae			
Sida rhombifolia L.	K.M. 58	Kaunzunzu	Rudérale
Mimosaceae			
Mimosa pigra L.	K.M. 59	Luute	Endroits sablonneux
Moraceae			
Ficus sp. 1	K.M. 68	Mulembo	Forêt secondaire
Ficus sp. 2	K.M. 36	Kambelangwa	Forêt secondaire
Musanga cecropioides R. Br.	K.M. 54	Musage	Forêt secondaire
Passifloraceae			
Passiflora foetida L.	K.M. 9	Libobe	Pionnière de jachère
Piperaceae			
Piper capense L. f.	K.M. 34	Nkesu	Forêt galerie
Piper umbellatum L.	K.M. 3	Mabilabondo	Forêt galerie
Poaceae			
Coix lacryma-jobis L.	K.M. 55	Nsambagele	Rudérale
Eleusine indica Gaertn.	K.M. 1	Kinsale	Rudérale
Paspalum conjugatum Berg.	K.M. 29	Bulambalamba	Rudérale
Rubiaceae			
Hymenodyction floribundum (Hochst. ex Steud.) Robinson	K.M. 53	—	Forêt dense sèche
Oldenlandia corymbosa L.	K.M. 30	—	Rudérale
Pauridiantha collicarpoides (Hiern) Bremek.	K.M. 20	Luunga	Pionnière de jachère
Pauridiantha dexevrei (De Wild. et Th. Dur.) Bremek.	K.M. 45	Kabile	Forêt secondaire
Spermacoce latifolia Aublet	K.M. 5	—	Rudérale
Sapindaceae			
Allophylus sp.	K.M. 46	—	Forêt secondaire
Solanaceae			
Solanum cf. *S. incanum* Domin	K.M. 14	Mukwanzala	Pionnière de jachère
Solanum nigrum L.	K.M. 70	Kasongo	Plante cultivée
Ulmaceae			
Trema orientalis Blume	K.M. 22	Munsonsoni	Forêt secondaire
Zingiberaceae			
Costus phyllocephalus K. Schum.	K.M. 11	Mugagegage	Forêt galerie

Toux

La toux se soigne en buvant la décoction de la tige de *Costus phyllocephalus* ou des fruits de *Piper capense.*

Hypertension artérielle

L'hypertension artérielle se soigne en mangeant les feuilles de *Piper umbellatum*, préalablement préparées à l'huile de palme, ou en buvant la décoction des feuilles de *Desmodium hirsutum* ou l'infusion de *Coix lacrima-jobis.*

Malaria cérébrale

Elle se soigne par lavement avec la décoction d'*Eleusine indica.*

Carie dentaire

La carie dentaire se soigne en appliquant sur la dent malade des feuilles écrasées de *Smilax kraussiana* ou de *Piper umbellatum.* On utilise encore de la même façon les caryopses de *Paspalum conjugatum* écrasés et mis auprès d'un feu doux.

Plaies

On applique sur la plaie la sève du *Ficus* sp. 2 ou la cendre de *Palisota ambigua.*

Gale et mycoses

Elles se soignent par application locale de racines écrasées de *Rauvolfia congolana.* On peut encore laver localement avec la décoction de *Hymenodyction floribundum.*

Abcés

Les abcès débutants sont résorbés par des pansements à base de feuilles de *Passiflora foetida.*

Rhumatisme et arthrite

Le membre malade est plongé pendant un certain temps dans une décoction d'une Sélaginelle. On peut encore réaliser un pansement avec les feuilles écrasées de *Lygodium microphyllum.*

Vaginite

Pour soigner la vaginite ou pour rendre le canal vaginal plus étroit on peut effectuer des lavages vaginaux, des lavements ou encore introduire des fruits écrasés dans le vagin. Les deux premiers traitements sont effectués avec l'infusion de *Phyllanthus muellerianus* ou de *Chenopodium ambrosioides.* Les fruits de *Piper capense* servent pour le dernier traitement.

Règles douloureuses et douleurs au bas-ventre

Ces affections se traiteent en buvant la décoction de *Thomandersia congolana*, l'infusion de *Tabernanthe iboga* ou de *Bidens pilosa.* On peut encore effectuer des lavements avec la décoction de *Smilax kraussiana.*

Préparation de la femme enceinte pour l'accouchement

Vers le huitième mois de grossesse, on fait des lavements avec la décoction de *Leea guineensis.*

Mammite

On applique sur les seins les feuilles de *Mimosa pigra* écrasées.

Favoriser ou provoquer la lactation

On donne à boire de l'eau de macération des feuilles de *Musanga cecropioides.*

Vermifuge

Pour tuer les vers intestinaux on écrase soit les graines du papayer (*Carica papaya*), soit les fruits de *Solanum nigrum*; cette mixture est allongée à l'eau et bue.

Impuissance fonctionnelle de l'homme

L'homme impuissant fume les fruits séchés de *Bidens pilosa.*

Affection cardiaque

Elle est combattue en buvant la décoction de *Lycopodium cernuum.*

Morsures de serpents

Les morsures de serpents sont combattues par application locale rapide d'un morceau de la tige d'*Alchornea hirtella.* Le traitement est suivi jusqu'à ce que le morceau tombe de lui-même.

2. *Plantes ichtvotoxiques*

Pour empoisonner les poissons, on écrase les feuilles de *Tephrosia* et on les trempe en amont du bief de la rivièra à traiter. On parcourt ensuite la rivière vers l'aval en attrappant les poissons étourdis ou morts

3. *Plantes à usage domestique*

Vannerie

Calamus deerratus constitue la corde principale utilisée pour les constructions de maisons, le tissage de paniers, de corbeilles et des chaises.

DISCUSSION ET CONCLUSION

Quarante-quatre plantes médicinales sont signalées pour la première fois du Maniema. Elles sont accompagnées d'indications précises concernant leur usage. Cette première contribution à l'ethnobotanique des Warega montre qu'au Maniema, comme ailleurs, la connaissance approfondie de la flore locale a été pendant de siècles à la base d'une phytothérapie variée. Plusieurs plantes de notre inventaire figurent dans d'autres études analogues, montrant par là, soit une circulation assez large de l'information, soit encore une découverte polytopique.

A la fin de ce travail,il nous semble essentiel d'insister encore sur l'absolue priorité de poursuivre rapidement de tels inventaires.

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Important indigenous plants used in the Transkei as food supplements

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ABSTRACT

Despite the fact that there is a tendency to rely more and more on foods which can be purchased at stores, the indigenous edible plants or veld foods play a significant role in the diet of the people living in the rural areas of the Transkei.

Although more work is required to gather and prepare veld foods, they can be an important and inexpensive source of macronutrients — carbohydrates, fats and protein — and also micronutrients such as minerals and vitamins.

Some of the more commonly-used plants such as *Sonchus asper, Chenopodium album, Centella coriacea, Galinsoga parviflora, Urtica urens* and *Solanum nigrum* are discussed and nutrient composition given. The names of a few plants which should rather be avoided, are also given.

Many of these edible plants are also regarded as weeds and, instead of eradicating them, their cultivation should perhaps be encouraged.

RÉSUMÉ

PLANTES INDIGÈNES IMPORTANTES AU TRANSKEI COMME SUPPLÉMENTS ALIMENTAIRES

Malgré le fait qu'il y ait une tendance à dépendre de plus en plus des aliments pouvant être achetés dans les magasins, les plantes indigènes comestibles ou aliments du veld jouent un rôle significatif dans l'alimentation des populations qui vivent dans les régions rurales du Transkei. Bien que plus de travail soit requis pour ramasser et préparer ces aliments du veld, ils peuvent être une importante et peu coûteuse source d'éléments macro-alimentaires, d'hydrates de carbone, de graisses et de protéines mais aussi d'éléments micro-alimentaires comme les minéraux et les vitamines.

Certaines des plantes les plus communément utilisées telles que Sonchus asper, Chenopodium album, Centella coriacea, Galinsoga parviflora, Urtica urens *et* Solanum nigrum *sont discutées et la composition alimentaire est donnée. Les noms de quelques plantes qui devraient plutôt être évitées sont également donnés.*

Beaucoup de ces plantes comestibles sont aussi considérées comme mauvaises herbes et, au lieu de les détruire, leur culture devrait peut-être être encouragée.

There is a tendency for the indigenous population groups of southern Africa, to forsake traditional veld foods and to rely more and more on foods which can be purchased from the local store. However, escalating prices of processed foods may force a reversal of this trend. Indigenous edible plants or veld foods still play a significant role in the diet of people living in the rural areas of the Transkei (Rose *et al.* 1974). Although they are seasonal, the variety of plants used ensures that some will be available throughout the year. The leaves of certain plants such as *S. nigrum* can be dried and kept for use during winter months. Green leaves, shoots, bulbs and roots are together a major food source, with wild and cultivated fruits forming a relatively minor part of the daily diet. Every housewife has to be able to distinguish the wild edible plants which she can use to supplement her diet and that of her family.

With the decreasing availability of animal protein, the value of these plants, which supply leaf protein in abundance, as a supplement to a staple diet of maize, cannot be overstressed. The quality of leaf protein is, of course, not the same as that of animal protein but, when the latter is in short supply, the judicious use of these indigenous plants can tide people over periods of famine. From the data given in Table 1 it is evident that plant leaves are also a good source of minerals, carotene, vitamin C and also contribute some B-vitamins to the daily diet.

In the Transkei there are over 100 different plants that are cooked as spinach with mealie meal *Zea mays* or used as relishes or side dishes. About 21 types of leaf are used as condiments, 23 roots and bulbs and 83 fruits are collected when available (Rose *et al.*, 1974). There are also some leaves, which are brewed as tea and used for medicinal purposes. Other potentially nutritious plants have to be avoided as they are poisonous.

1. *Imifino plants*

The types of 'imifino' or plants used as a spinach or pot herb can be divided into three categories:

1.1 *Commonly-used plants that are safe to use*

Sonchus asper — irwabe
Chenopodium album — imbikikane
Centella coriacea — onongotysana

1.2 *Commonly-used plants that are not always safe to use*

These plants must be picked with care, as some of the Xhosa names are interchangeable with those of

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TABLE 1. – Composition of leaves and fruits. (Results expressed on natural basis.)

Description of Material	g/100 g						kJ/100g	mg/100 g													I.U./ 100g
	Moisture	Ash	Protein	Fat	Fibre	Carbohydrate	Energy value	Ca	Mg	Fe	Na	K	Cu	Zn	P	Thiamin	Riboflavin	Nicotinic acid	Vit. C	Carotene	Vit. A Activity
Irhwabe (*Sonchus asper*)	87,7	3,7	2,8	0,5	2,0	5,9	164	237,00	67,0	14,90	121,00	422	0,44	0,80	40,0	0,05	0,16	0,64	–	–	
Imbikicane (*Chenopodium album*)	83,6	3,6	4,7	0,3	1,7	6,7	200	239,00	162,0	4,80	9,90	833	0,25	2,00	76,0	0,03	0,23	0,71	8,0	6,0	10 000
Unongotyozana (*Centella coriacea*)	81,5	3,2	3,0	1,0	2,4	9,0	238	239,00	101,0	19,70	311,00	327	0,30	3,01	30,9	0,06	0,23	0,80	23,0	2,8	4 667
Umsobo wehlathi (*Solanum 'nigrum'* complex)	82,5	2,6	3,9	0,7	2,6	7,6	219	213,00	98,7	8,60	–	512	0,33	1,12	25,5	0,07	0,20	0,44	2,1	4,4	7 333
Idolo lenkonyane (*Rumex ecklonianus*)	82,8	1,9	4,6	0,7	1,8	8,0	240	111,00	85,0	9,70	14,00	693	0,13	2,40	74,1	0,16	0,17	1,54	–	–	
Unompontshane (*Galinsoga parviflora*)	88,4	1,7	3,2	0,4	1,1	5,2	156	284,00	60,0	5,30	2,30	351	0,33	1,30	58,0	0,08	0,21	1,21	6,7	4,0	6 667
Umva wamadoda (*Erigeron bonariensis*)	79,4	3,4	3,6	0,4	2,9	10,3	249	292,00	96,9	17,00	79,90	746	0,57	3,01	54,4	0,08	0,21	0,98	17,0	5,6	9 333
Iguzi (*Physalis viscosa*) leaves	82,8	2,7	4,9	0,6	1,7	72,0	226	151,00	110,0	21,60	183,00	748	0,26	1,30	65,6	0,12	0,25	1,33	–	–	–
Iguzi (*Physalis viscosa*) berry	78,8	1,4	2,2	1,3	–	–	–	9,34	28,8	1,13	3,55	581	0,59	0,64	52,0	–	–	–	50,0	2,3	3 833
Irawu (*Urtica urens*)	80,2	4,7	5,2	0,6	2,9	7,1	232	528,00	127,0	7,20	51,60	553	0,28	0,57	112,0	0,03	0,33	1,21	2,1	4,9	8 167
Inkwandlakwandla (*Senecio albanensis*)	86,3	2,6	2,6	0,7	1,9	5,9	169	199,00	73,9	15,10	3,90	389	0,37	0,07	53,8	0,08	0,16	0,90	14,0	4,6	7 667
Strawberry guava (*Psidium littorale*)	80,4	0,8	0,7	0,6	6,2	11,3	276	82,90	42,1	0,73	59,20	219	0,17	0,22	15,0	0,08	0,02	0,37	19,0	–	–
Wild fig (*Ficus* sp.)	87,4	0,8	1,3	0,8	3,0	6,7	165	36,90	27,8	0,67	4,81	333	0,17	0,45	36,0	0,06	0,01	0,40	3,0	–	–
Umbhongisa (*Diospyros dichrophylla*)	63,7	2,4	1,7	0,1	1,1	31,0	553	30,90	38,6	0,97	–	444	0,23	0,34	20,6	–	0,004	0,29	41,4	–	–
Isiqwashumbe (*Raphanus raphinastrum*)	87,4	3,1	3,7	0,3	1,4	4,2	142	285,00	98,9	9,51	6,80	530	0,18	1,36	54,6	0,07	0,14	0,62	11,0	1,8	3 000

inedible species and/or because there are times of the year when the plants are toxic. The majority of these plants belong to the Amaranthaceae.

Pigweed or hanekam *(Amaranthus paniculatus)* is called utyuthu, unomdlomboyi or imbuya and ujigenxawini in the Mount Fletcher district. The small pigweed *(Amaranthus thunbergii)* is also called utyuthu or unomdlomboyi. In some parts of the Transkei the name umambumbu is used for both *A. paniculatus* and *A. thunbergii*. Then *A. blitum* is also known as unomdlomboyi.

Most of the *Amaranthus* and *Chenopodium* species are nitrite accumulators. Only the early and young green shoots of these plants should be eaten.

Both the leaves and ripe berries of umsobo (a name applied to several species in the *Solanum nigrum* complex) are nutritious and a popular item in the diet. However, the unripe fruits are poisonous due to toxic alkaloids.

1.3 *Less commonly-used 'imifino' (presumed safe)*

Rumex ecklonianus — idolo lenkonjane
Galinsoga parviflora — unompotsane
Erigeron bonariensis — umvamadoda
Raphanus raphinastrum — isiqwashumbe
Physalis viscosa — iguzi
Urtica urens — irhalijane

2. *Plants which should be avoided at all times as they contain toxic alkaloids*

Senecio albanensis — impondlapondla
inkwandlakwandla
S. deltoideus — undenze
ityholo
Pachycarpus sp. — itshongwe
Solanum incanum — umthuma
Solanum aculeastrum
Cassine capensis — umbovane

The species of *Senecio* contain pyrrolizidine alkaloids which are liver toxins and may cause liver cancer (Rose, 1972). *Solanum incanum* contains nitrozamines which are notorious for their cancer-inducing properties.

3. *Plants used as a relish to give a bitter taste to maize meal*

Especially leaves of:
Physalis peruviana — iguzi
Prunus persica — ipisika

In Table I the composition of leaves of some of these plants and a few fruits which have been analysed in the laboratories of the National Food Research Institute of the CSIR, are given.

These leaves are usually eaten in some or other cooked form in conjunction with white maize meal porridge. The latter is a poor source of protein, calcium, iron, zinc, riboflavin, nicotinic acid and contains no vitamin C or carotene (pro-vitamin A). Maize meal porridge is a good source of magnesium, potassium and thiamin, but a fair amount of the phosphorus is in the form of phytic acid which is not available to the body. Phytic acid can also combine with calcium, magnesium, iron and zinc to form the insoluble salts which are then unavailable to the body. Phytic acid occurs mainly in the maize bran and, although it has not been determined in these plants, one can assume that very little, if any, should be present.

From the figures given in Table 1, it is evident that these plants supplement protein to some extent and that they are a good source of minerals, especially calcium, of which maize is a very poor source. Riboflavin and nicotinic acid are well supplemented and, of course, vitamin C and carotene. The latter, especially β-carotene, is converted to vitamin A in the body which is stored in the liver and can tide people over in the winter months.

When planning a health programme for the Transkei, these indigenous plants should not be ignored as they are a good source of food, require no special cultivation or care. They are there for the picking when more expensive to grow and, sometimes, less nutritious, garden vegetables are unobtainable. Many of these plants are regarded as weeds and their eradication is sometimes advocated. Perhaps their cultivation should rather be encouraged.

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Quelques vertus médicinales de *Cassia occidentalis* L. (Césalpiniacées) en basse Côte d'Ivoire

L. AKÉ ASSI*

RÉSUMÉ

Une quarantaine d'espèces de *Cassia*, parmi lesquelles plusieurs sont introduites, poussent dans les diverses régions de l'Afrique intertropicale, dans tous les groupements végétaux.

Les représentants ivoiriens, au nombre de 14, sont des herbes, des plantes suffrutescentes, des arbustes ou des arbres. La pharmacopée locale utilise 6 de ces plantes pour diverses préparations thérapeutiques.

L'espèce la plus couramment employée est *Cassia occidentalis* Linn., vulgairement appelée Faux Kinkéliba. On compte, dans la région forestière de la Basse Côte d'Ivoire, 11 recettes médicamenteuses dans lesquelles interviennent les diverses parties de la plante.

Douée d'un grand pouvoir d'expansion, cette plante sud-américaine est devenue de ce fait, pantropicale. On la rencontre surtout aux abords des villages.

On l'emploie pour soulager les maux les plus divers et pour d'autres causes: comme abortif, cicatrisant, diurétique, fébrifuge, laxatif ou cholagogue, reconstituant, contre l'albuminurie, l'asthme, la cataracte, la jaunisse, le kwashiorkor.

ABSTRACT

SOME MEDICINAL PROPERTIES OF CASSIA OCCIDENTALIS *L. (CAESALPINIACEAE) IN THE LOWER IVORY COAST*

About 40 species of Cassia, *a great number of which have been introduced, grow in different parts of intertropical Africa, in all types of vegetation.*

The 14 species in the Ivory Coast are herbs, shrubs or trees. The local pharmacopoeia uses six of these species for various therapeutic preparations.

The currently most used species is Cassia occidentalis *L. commonly called Faux Kinkéliba. In the forest area of the Lower Ivory Coast, 11 medical preparations made from different parts of the plant are used. With its considerable ability to spread, this South American plant has become a pantropical one. It is found chiefly in the vicinity of villages.*

C. occidentalis *is used for the relief and treatment of a variety of pains and diseases, for example as a cicatrizant, abortifacient, febrifuge, diuretic, laxative or cholagogue and tonic, and in cases of asthma, cataract, jaundice and kwashiorkor.*

INTRODUCTION

Le genre *Cassia* renferme environ 700 espèces réparties dans les régions tropicales et subtropicales du monde.

Une quarantaine d'espèces, parmi lesquelles plusieurs sont introduites, poussent dans les diverses régions de l'Afrique intertropicale, dans tous les groupements végétaux.

Les représentants ivoiriens, au nombre de 14, sont des herbes, des plantes suffrutescentes, des arbustes ou des arbres. La pharmacopée locale utilise 6 de ces plantes pour diverses préparations thérapeutiques.

Mais l'espèce la plus couramment employée est *Cassia occidentalis* L., le Faux Kinkéliba. On compte, dans le région forestière de la basse Côte d'Ivoire, 11 recettes médicamenteuses dans lesquelles interviennent les diverses parties de la plante.

Cassia occidentalis *L.* Sp. P1. ed. 1: 377 (1753); DC., Prodr. 11: 497 (1847); Oliver, F.T.A. 2: 274 (1871); Keay, F.W.T.A. ed. 2, 1: 455 (1958).

Cassia planisiliqua Linn., Sp. P1. ed. 1: 377 (1753).

Plante suffrutescente, atteignant de 0,50 à 1,50 m de haut, glabrescente. *Feuilles* paripennées, de 15 à, 20 cm de long, odorantes; pétiole et rachis légèrement canaliculés au-dessus; grosse glande brune à la base du pétiole; folioles lancéolées, oblongues-lancéolées ou ovées, de 5 à 10 cm de long, et de 2 à 3 cm de large, glabrescentes à glabres, peu ciliées, acuminées, disymétriques à la base; pétiolule courte; nervures latérales de 8 à 10 paires. *Inflorescences* axillaires, courtes, 2ˉ – 4ˉ flores. *Fleurs* jaunes, atteignant 1 cm de long; sépales elliptiques, inéguax; pétales obovales, onguiculés; étamines 6, les 2 inférieures plus grandes, atteignant 12 mm de long, les 4 moyennes de 6 à 7 mm de long; 1 étamine staminodiale entre les 2 étamines inférieures; 3 staminodes ovales; ovaire linéaire, 7 mm de long, pubérulent; style 4 mm de long, arqué, à stigmate latéral, pilleux. *Gousses* subcylindriques ou aplaties, droites ou légèrement falciformes, apiculées, glabrescentes ou glabres, de 10 à 12 cm de long, jusqu'à 6 mm de large. *Graines* nombreuses, aplaties, brunâtres, grisâtres en vieillissant,disposées transversalement dans le gousse. Fig 1.

Originaire de l'Amérique de Sud, le Faux Kinkéliba est doué d'un grand pouvoir d'expansion. Il est devenu de ce fait, une espèce pantropicale.

Noms vulgaires: Faux Kinkéliba, Herbe puante, Café nègre.

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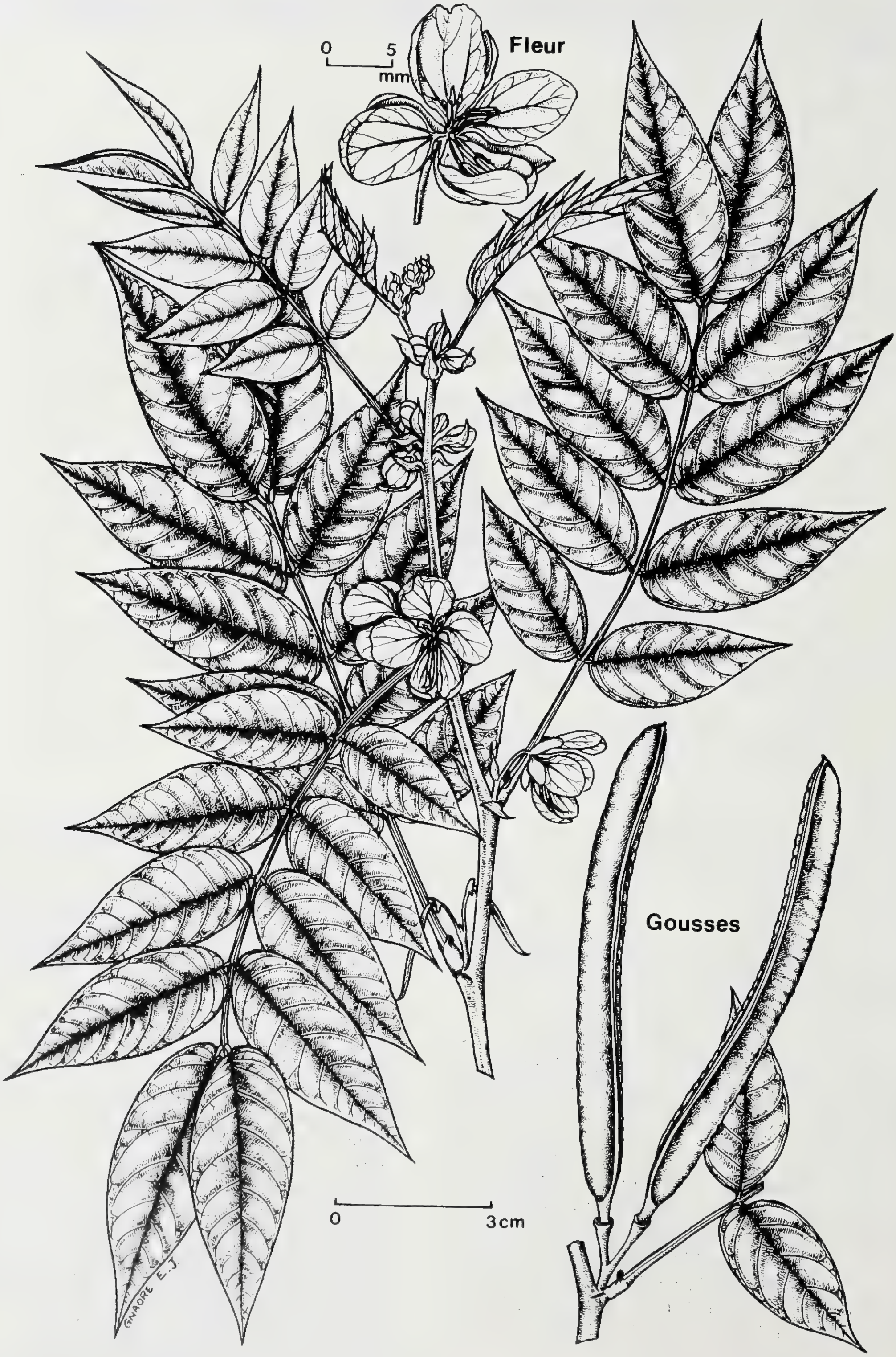

Fig. 1.—*Cassia occidentalis* L.

Noms vernaculaires: Gbébé n'dé (abbey); M'Bèchilè Gnilè-té (attié); Badja (Malinké); Alouklou-Sèrè-Sèrè, Sango-Sèrè-Sèrè (baoulé); Sèrè-Noumbrou (Orodougou).

USAGES

Les différentes parties de la plante entrent dans la préparation de plusieurs remèdes couramment utilisés pour soulager les maux les plus divers et pour d'autres causes (Tableau 1).

Abortif

On recommande en lavement, 3 fois par jour (matin, midi et soir), le produit de décoction des racines de la plante. Pour plus d'efficacité, il est conseillé de retenir le liquide, assez longtemps, dans le rectum avant son évacuation.

Albuminurie

Prendre en boisson, plusieurs fois par jour, la décoction des feuilles.

Asthme

Le produit de macération des feuilles est conseillé en boisson (matin, midi et soir) au malade pendant plusieurs jours.

Pour obtenir le produit, triturer les feuilles dans de l'eau froide, filtrer après 2 ou 3 heures de temps, quand le liquide prend une teinte verte.

Cataracte

Administrer en instillations oculaires, trois fois par jour (matin, midi soir) l'extrait des feuilles de la plante. Le produit s'obtient en écrasant les feuilles de Faux Kinkéliba et une gousse de Poivre de Guinée (*Xylopia aethiopica*) avec un peu d'eau.

Cicatrisant

Comme cicatrisant de la plaie du cordon ombilical, on utilise les fleurs de la plante. Pétrir celles-ci, incorporer dans cette pâte du beurre de karité. Faire le pansement matin et soir jusqu'à cicatrisation complète.

Diurétique

Prendre en boisson, le soir, une quantité importante d'infusion ou de décoction des feuilles de la plante.

Fébrifuge

Absorber un grand verre, le matin, midi et soir, de décoction des feuilles de Faux Kinkéliba. Faire un bain de vapeur et se laver matin et soir avec cette même décoction.

Jaunisse (= Djèkouadjo)

Boire un grand verre, matin, midi et soir, du produit de décoction des feuilles de la plante. On conseille de faire un bain de vapeur et de se laver avec le même produit, matin et soir, jusqu'à rétablissement.

Kwashiorkor

La décoction des raciness de la plante est donnée en boisson au malade 3 fois par jour (matin, midi et soir) jusqu'à guérison.

Laxatif ou Cholagogue

Le produit de macération, des feuilles dans de l'eau froide, est conseillé en lavement le soir.

La pâte obtenue après écrasement des feuilles et délayée dans de l'eau tiède, donne solution verte qui, administrée en lavement, facilite l'évacuation des voies extra-hépatiques.

Reconstituant

La décoction des feuilles du Faux Kinkéliba, avec des portions de fruits mûrs d'Ananas, constitue une boisson efficace contre la jaunisse, ainsi que contre la fatigue générale. C'est un très bon remontant.

TABLEAU 1.—Résumant certaines causes et le mode le leur traitement par les diverses parties de *Cassia occidentalis* L. (Césalpiniacées)

Causes de l'utilisation de la plante	Parties utiles de la plante et modes de leur utilisation																					
	Feuilles												Fleurs	Racines								
	Macération				Extrait				Décoction et Infusion				Extrait	Macération			Extrait			Décoction et Infusion		
	1	2	3	4	1	2	3	4	1	2	3	4	Pansement	1	2	3	1	2	3	1	2	3
Abortif																						+
									+													
Asthme	+																					
Cataracte								+														
Cicatrisant											+											
Diurétique									+													
Fébrifuge									+	+												
Jaunisse (Djèkouadjo)									+	+												
Kwashiorkor																				+		
Laxatif ou chalogogue			+				+															
Reconstituant	+																					

Les chiffres indiquent: 1 = boisson, 2 = Bain, 3 = lavement, 4 = instillation oculaire.

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A survey of ethnobotanical research in southern Africa

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ABSTRACT

Existing ethnobotanical information for southern Africa is scattered through anthropological, medical, botanical and other books and journals, making the task of getting at the information fairly difficult. The object of this paper is to provide a unified bibliography on the subject and to review the state of knowledge of ethnobotany in southern Africa as reflected in publications, unpublished manuscripts and museum and herbarium holdings. Those aspects of ethnobotany most needing attention are identified. The information is reviewed on a subject basis.

RÉSUMÉ

UN RELEVÉ DE LA RECHERCHE ETHNOBOTANIQUE EN AFRIQUE AUSTRALE

L'information ethnobotanique existant pour l'Afrique australe est dispersée parmi des livres et journaux anthropologiques, médicaux, botaniques et autres, ce qui rend la tâche d'obtenir cette information, assez difficile. L'objet de ce document est de fournir une bibliographie unifiée sur le sujet et de faire un relevé de la connaissance de l'ethnobotanique de l'Afrique australe telle qu'elle est réfléchie dans les publications, les manuscrits non publiés et les collections de musées et d'herbarium. Les aspects de l'ethnobotanique nécessitant le plus d'attention sont identifiés. L'information est revue par matières.

INTRODUCTION

Ethnobotany was defined as early as 1895 as the study of 'plants used by primitive and aboriginal peoples' (Ford, 1978, p. 33). This encompasses an enormous field of research. Ford has defined the limits of this field on the basis of three objectives.

1. to identify plants that have uses
2. to discover how people classify, identify and relate to these plants
3. to examine the reciprocal interactions of plants and people.

Most of the ethnobotanical work done in southern Africa satisfies only the first of Ford's objectives, although there is some that satisfies the second and even the third.

The purpose of this paper is to review the state of knowledge of ethnobotany in southern Africa as reflected in publications, unpublished manuscripts, museum and herbarium holdings. Ethnobotanical research has been carried out by missionaries and explorers, botanists, medical people and anthropologists, hence the published information is found in a variety of books and journals. The peoples covered by this review are the indigenous peoples of southern Africa: the San (Bushmen), the Khoi (Hottentots) and the Bantu — the latter comprising the South Sotho, North Sotho, Tswana, Zulu, Cape Nguni, Swazi, Transvaal Ndebele, Tsonga/Tonga, Venda, Ambo, Herero and Mpukushu.

The uses of plants will be reviewed under the following headings: food; medicine; magic, ritual and customs; building; household utensils and implements; musical instruments; and firewood and firesticks.

FOOD

Early records of plants used for food and drink by the Khoi and Bantu of the Cape occur occasionally in the journals of travellers such as Burchell (1822), Campbell (1822) and Chapman (1971). For Kaffraria (Eastern Cape) Kay (1833) and Ayliff (1858) noted commonly used plant foods. Mayr (1906) describes some of the food plants of the Zulu. Subsequently, up to the middle 1950's, accounts of both cultivated and wild foods appeared. Beer- and wine-making are described by Fox (1938) and Turner (1909). The food uses of particular species are discussed by MacCrone (1937), Van der Bijl (1921) and Watt (1926). Anthropological monographs also include some information; Junod (1962) mentions some Tsonga food plants and Stayt (1968) some Venda food plants.

The general diet of various peoples was also studied; of note is the work on the South Sotho (Ashton, 1939), the Swazi (Beemer, 1939) and the Zulu (Bryant, 1939).

1957 seems to mark the beginning of a new phase of research on food plants and plant-based subsistence, particularly of the hunter-gatherer San of the Kalahari. No less than 25 books, articles and manuscripts have appeared since then, dealing, wholly or in part, with San subsistence, particularly gathering of wild plant foods. Important contributions are those of Lee (1965, 1958, 1969, 1972, 1973), Maguire (1978), Marshall (1965, 1976), Silberbauer (1965, 1972), Steyn (1971, 1981), Story (1958) and Tanaka (1969, 1972, 1976). Dentlinger (1977) studied the role of the plant *Acanthosicyos horrida* in Topnaar Khoi life.

There has also been considerable interest in and research on Bantu foods, including traditional crops. There are accounts of the traditional diets of the North Sotho (Franz, 1971; Quin, 1959), the Tembe-Tonga (Lubbe, 1971) and the Cape Nguni (Rose, 1972a). Wild plants collected as food are

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recorded by Jacot Guillarmod (1966) (South Sotho), Rose (1972(b)) and Rose & Jacot Guillarmod (1974) (Cape Nguni) and Van der Merwe *et al.* (1967) (Tonga of north-eastern Natal).

Food plants are also mentioned in the anthropological works of Hammond-Tooke (1974) and Mönnig (1967); in botanical works such as Jacot Guillarmod (1971) and Palmer & Pitman (1972); and in Malan & Owen-Smith's (1974) ethnobotanical study of the Herero. Besides the published works there are numerous reports and unpublished manuscripts listing edible plants, some of which are; Bridges (1977), Grivetti (1975) and Hitchcock (1977a; 1977b; 1978) for the Tswana; Garland (1971) and Waugh (1970) for the Zulu.

The nutritional value of some of these edible wild plants has been investigated; fruits by Engelter & Wehmeyer (1970), Wehmeyer (1966, 1976) and Wehmeyer, Lee & Whiting (1969); leaves by Fox (1966), Hennessey & Lewis (1971), Levy, Weintroub & Fox (1936), Lewis, Shanley & Hennessey (1971) and Shanley & Lewis (1969). In press at present is a book by F. W. Fox on veld foods. A. S. Wehmeyer of the CSIR has analysed many wild food plants, but only some of the data have been published.

The National Herbarium, Pretoria, includes many collections of edible plants with notes on their use. This information has recently become available as a result of the computerization of the Herbarium. Some of this information has not yet been published, such as that collected by Rodin (Ambo), Hemm (Venda), Barnard and Mogg (North Sotho). Other information, like that collected by Gerstner (Zulu), Miller (Tswana), Story and Maguire (San), has been at least partially used in reports and publications.

In summary — the gathering of wild food plants by the hunter-gatherer San has been well studied. The traditionally cultivated crops and wild plants collected as supplementary foods of the Zulu, Cape Nguni, South Sotho and North Sotho are also relatively well recorded. For the Swazi, Tsonga, Tswana, Venda, Herero and Owambo less is known. Except for the records of early travellers and one recent piece of work, little is known of Khoi food plants. Nothing has been recorded for the Transvaal Ndebele.

MEDICINE

The recording of the medicinal uses of plants began early at the Cape. Thunberg (no date) and Lichtenstein (1928), while on their travels, noted uses of medicinal plants. In 1795 Berg, a student of Thunberg, defended a dissertation on African medicinal plants (Berg, 1799). Pappe's 'Florae Capensis Medicae Prodromus', first published in 1850 collates all the scattered notes of Lichtenstein and Thunberg, adding also later information, derived mostly from the manuscript notes of a Dr MacKrill who collected information on medicinal plants during the period 1814–1816 (MacOwan, 1897).

Burchell (1822), Kay (1833) and other travellers and explorers also recorded Khoi, Cape Nguni and Tswana medicinal uses of plants. A major nineteenth century contribution is that of Smith (1888) on the medicinal plants of the eastern Cape.

Twentieth century research can be divided into two phases, with the appearance of the second edition of Watt & Breyer Brandwijk (1962) as the watershed. During the first period many articles were published, mostly in scientific and medical journals, dealing with various aspects of medicinal plants, including: analyses of chemical composition and pharmacological action (Brandwijk & Watt, 1925; Frost, 1941; Jamieson, 1917; Lewis & Gibbs, 1921; Stephen-Lewis, 1936; 1938); poisonings due to the administration of medicines (Gordon, 1947; Juritz, 1915; Sapeika, 1944); and many general notes on plant-derived medicines. The latter include accounts of Tsonga medicinal plants (De Almeida, 1930), Zulu (Bryant, 1966; Mayr, 1906), Khoi (Dornan, 1924; Laidler, 1928), Ambo (Loeb, 1956), Tswana (Lebzelter, 1933), Ndebele (Watt & Van Warmelo, 1930) and South Sotho medicinal plants (Laydevant, 1933, 1939, 1943; Watt & Breyer Brandwijk, 1927a; 1927b; 1928).

Schapera (1930) recorded the use of 10 plants for protecting and healing cattle. Several anthropological works published in that period contain fairly good records of medicinal plant uses, for example, Ashton's (1952) word on the South Sotho, Junod's (1962) on the Tsonga, Mayr's (1906) on the Zulu and Stayt's (1968) on the Venda. Some botanical works also contain useful information (Miller, 1948; Phillips, 1917). Annotated checklists of plant names in the various languages also have notes on medicinal uses of plants. An example is Gerstner's (1938) checklist of Zulu names, based on an extensive collection of plants housed in the National Herbarium.

Other collections of medicinal plants in the herbarium are those of Alice Pegler, O. B. Miller, H. H. Curson, W. G. Barnard, W. J. Hanekom and, of course, J. M. Watt and M. G. Breyer Brandwijk.

The latter two people made the most important contribution to the study of medicinal plants in southern Africa. Besides producing several articles and making an extensive collection of medicinal plants, they collated all that was known on the subject up to 1932 in the 'Medicinal and Poisonous plants of Southern Africa'. In 1962 this was succeeded by the monumental revised and expanded second edition (Watt & Breyer Brandwijk, 1962).

Since then, there has been continued interest in medicinal plants. Tswana medicinal plants have been studied by Teichler (1971a, 1971b) and Reynecke (1971). This latter piece of work is a detailed account of medicine and magic, including much information on medicinal plants, their uses and preparation. A large collection of medicinal plants was made by Reynecke. This collection is housed in the National Herbarium.

Jacot Guillarmod (1971) includes in the list of plant uses in 'Flora of Lesotho' a large number of plants used for medicinal purposes by the South

Sotho. North Sotho medicinal plants have been recorded by Mönnig (1967) and Hanekom (1967). Rose (1972(a)) has recorded the use of some *Senecio* species as medicines and Ngubane (1977) gives a few examples of medicinal plants and their preparation. Liengme (1981) includes a number of plants used medicinally by the Tsonga. Some Herero medicinal plants are discussed in Malan & Owen-Smith (1974).

Two recent collections of medicinal plants in the National Herbarium are those of R. J. Rodin (Ambo) and J. W. Snyman (Tswana).

In general, the medicinal use of plants of most of the cultural groups has been reasonably well studied, particularly that of the Zulu and South Sotho. The Venda, Tsonga and North Sotho of the Transvaal and the Swazi warrant some research. Two groups for whom very little is known regarding medicinal plants are the Khoi and San.

Other aspects of plant utilization have received far less attention than these first two.

MAGIC, RITUAL AND CUSTOMS

Although not always clearly separated from medicinal uses, magical uses are here dealt with as a different aspect of plant use. Magic trees of the Bantu are dealt with by Friede (1956) and Watt (1956), and plants used in Cape Nguni magical charms are touched on briefly by de Jager (1963) and de Lange (1961). Rituals often involve the administration of magic medicines and some of these are recorded for the Tsonga (Johnston, 1972), the South Sotho (Laydevant 1932; 1939), the Ambo (Loeb, 1955) and the Tswana (Schapera 1932). Other ritual uses of plants are mentioned very briefly in Kuper (1944) and Schoeman (1937) (Swazi) and Willoughby (1905) (Tswana). Rainmaking ceremonies involve plants, too (Dornan, 1929; Schapera, 1971). Specific plants are customarily associated with twins, as recorded by Cook (1927) for the Cape Nguni and Dornan (1932). There are also a few records of sacred plants in the literature. Dicke (1926) discusses a Venda sacred plant; Laydevant (1946) Sotho sacred plants. Customs protecting trees are discussed by Ferreira (1948).

Some of the sources referred to under medicinal uses also include information on magical uses of plants, e.g. Jacot Guillarmod (1971), Gerstner (1938), Miller (1952), Reynecke (1971) and Stayt (1968).

BUILDING

In a compilation of records on Cape Nguni (Xhosa) settlement, Shaw & Van Warmelo (1972) include a few references to plant materials used in building huts, fences and stockades. Many of the early accounts included in the compilation only describe these structures and sometimes give the building materials as 'wood' or 'grass'.

The few other records that exist include a detailed account of the materials used to build a dome-shaped grass hut in Natal (Knuffel, 1973), a discussion of Tswana thatching grasses (Van Voorthuizen & Odell, 1976), accounts of Tswana building (Van Voorthuizen, 1976; Snyman, 1977) and Malan & Owen-Smith's (1974) notes on Herero building. Some botanical sources contain relevant information, e.g. Palmer & Pitman (1972).

R. J. Rodin's Owamboland collection, housed in the National Herbarium, includes plants used in building.

HOUSEHOLD UTENSILS AND IMPLEMENTS

Hunting and fishing equipment

The hunting equipment of the San is to a large degree made from plant materials and some of these are discussed in a number of publications on San subsistence ecology (Lee, 1965; 1972; Silberbauer, 1965, 1972; Steyn, 1971; Story, 1964; Tanaka, 1976) and also briefly in Dornan (1975). Plants providing arrow poisons have long attracted the attention of researchers and records of these are well documented in Shaw, Wooley & Rae's (1963) review of San arrow poisons.

For the Bantu, there are a few references to the use of plants for spears and knob-kieries in the standard anthropological works (e.g. Junod, 1962; Mönnig, 1967; Stayt, 1968). Herero weapons are included in Malan & Owen-Smith (1974). Fishing equipment of southern African people in general is discussed by McLaren (1958). Tinley (1964) gives a detailed account of plants used to manufacture Tonga fishing equipment. Trees used for making canoes in the Okavango Delta are listed by Larson (1975).

Baskets and mats

Some plants used for mats and basketry are mentioned in anthropological works, but more often than not the materials are only identified as 'grasses', 'lianas' and 'reeds'.

Gerstner (1938) lists some plants used by Zulu, as do McLaren (no date), Steer (1980) and Grossert (1968), who also discusses some taboos regarding these plants. Shaw & Van Warmelo in their review of Cape Nguni crafts list some of the plants used in basketry. A few basketry-plants used by the Tswana are mentioned by Lamprecht (1976); some used by the Tsonga are given in Liengme (1981); whilst Malan & Owen-Smith (1974) includes some Herero basket-plants. Jacot-Guillarmod's (1971) 'Flora of Lesotho' contains considerable information on this aspect of plant use.

There are a few collections in the National Herbarium; two important ones being those of W. G. Barnard (North Sotho) and R. J. Rodin (Ambo). Miss E. M. Shaw of the South African Museum has been studying basketry for many years and has collected a lot of information on plant materials used.

Wooden utensils and implements

Malan & Owen-Smith (1974) give a good deal of information on the various woods used for household purposes by the Herero. Ferreira (1928) and Van Voorthuizen (1976) mention a few woods used by the Tswana; Gerstner (1938) includes woods used by the Zulu and Shaw & Van Warmelo (1974) contains a list of some woods used by the Cape Nguni. Swazi and Tsonga use of woods are mentioned in Codd's (1951) book on Kruger National Park Trees, and more information on Tsonga wood use for household purposes is given in Junod (1962) and Liengme (1981). Palmer & Pitman (1972) has a lot of general information on the subject.

Unpublished information has been gathered by Snyman, and in the National Herbarium are collections by R. J. Rodin and E. M. Loeb. Lindsay Hooper of the South African Museum has recently completed a review of wood-working amongst the Nguni groups.

Miscellaneous other household uses

Plant-derived dyes used by the Zulu are listed in Mtshali (1927), Nixon (1942) and Xaba (1923).

Cosmetic uses of plants are briefly mentioned by De Lange (1963), Jacot Guillarmod (1971) and Gerstner (1938). The cosmetic plants of the Ambo and Herero are dealt with in some detail in Loeb, Koch and Loeb (1956) and Malan & Owen-Smith (1974) respectively.

Beads, oil, soap, toys, clothing and ornaments are other uses of plants which are occasionally recorded, e.g. in Malan & Owen-Smith (1974), Snyman (no date), Jacot Guillarmod (1971) and Gerstner (1938).

The cultivation and use of calabashes *(Lagenaria siceraria)* by the Nguni groups is well documented by Böhme (1976), and a few of the plants used in skin-working by the Zulu and North Sotho are recorded by Vaughan-Kirby (1918) and Shaw & Böhme (1974).

MUSICAL INSTRUMENTS

R. P. Kirby, in his many years of work on African music, noted several of the plant materials used in making musical instruments (Kirby, 1932, 1934, 1943). In a paper on reed flute ensembles (Kirby, 1933) he discusses the taboos and rites involved in the cutting and making of Venda bamboo flutes. Van Warmelo (1932) also has some notes regarding this. San musical instruments are discussed by Nurse (1972) and Tswana instruments by Wood (1976). A few plants used in Tsonga musical instruments are recorded by Junod (1962) and Liengme (1981). Jacot Guillarmod (1971) includes a few plants used by the South Sotho.

FIREWOOD AND FIRESTICKS

This aspect of plant utilization is often overlooked. There are some references to woods avoided as firewood for various reasons (Ferreira, 1949; Friede, 1953) and a few to woods used, and even preferred, as fuel (Snyman, no date; Malan & Owen-Smith, 1974; Jacot Guillarmod, 1971; Best, 1979; Liengme, 1981). De Vaal (1942) mentions a few woods used by the Venda for iron-smelting. Woods used to start fires (fire-sticks) by the Herero are given in Malan & Owen-Smith (1974). Friede (1979) has gathered together numerous scattered records of fire-sticks.

SUMMARY OF USES

Medicinal and food plant uses of most of the indigenous peoples have been, on the whole, well documented. An exception are the Khoi, for whom little has been recorded since the early travellers in the Cape like Campbell and Burchell.

Some magic, ritual and customary uses of plants of a number of the cultural groups have been recorded, but no one group has been well researched, except perhaps, the Tswana.

Plants used in all the various aspects of the material culture of the different peoples are, in general, poorly researched. Some plants used in building, basketry, wooden utensils and household implements, musical instruments and various other uses like dyes and cosmetics are recorded for most of the cultural groups; but there are few substantial accounts of these.

FOLK TAXONOMY AND PLANT LORE

Many plant names in the various languages have been collected. These are generally incorporated in the various dictionaries (e.g. Cuenod, 1976; Doke & Vilakazi, 1964; Van Warmelo, 1937) or are published in botanical works (e.g. Compton, 1966; Jacot Guillarmod, 1971). Several lists of vernacular plant names have also been published on their own (e.g. Beyer, 1920; Gerstner, 1938; Paroz, 1962). There are also unpublished lists of names (Henkel, Tait & Edwards, no date; Baumbach, 1966; Snyman, no date). A computer search of the National Herbarium data bank has produced a large pile of print-out that still has to be looked through.

There have been few studies of the principles of plant classification and naming. Junod (1962) has a short discussion of Tsonga classification and Malan & Owen-Smith (1974) touch on Herero folk taxonomy.

A detailed account of folk botany and plant lore of the !Ko San is given in Heinz & Maguire's (no date) paper on !Ko ethnobiology. They discuss not only nomenclature and taxonomy but also recognition of plants and conceptualization of botanical phenomena.

MAN-PLANT INTERACTIONS

In their account of Herero ethnobotany, Malan & Owen-Smith (1974) discuss some of the effects of plant utilization by man on the environment. This is the only account of this aspect of ethnobotany. There are at present two projects being undertaken on wood utilization and its effects — one amongst the Tsonga of north-eastern Transvaal and the other amongst the Zulu of northern Natal.

DISCUSSION AND CONCLUSIONS

The primary focus of ethnobotanical research in southern Africa has been on identifying plants that have uses, with the concomitant recording of the vernacular names of these plants. This review has shown that it is only medicinal and food uses of plants that have been well-studied, and that all other aspects of plant use require additional research. This is not to say that there is nothing new to learn regarding medicinal and food plants — the diversity of both vegetation and peoples in southern Africa implies a potentially vast amount of information to be recorded.

Of the aspects of plant use requiring research, it is the many and diverse uses of wood that most need investigation; for example woods used in traditional musical instruments need to be recorded, since these are rapidly being replaced by instruments made of materials other than wood, or by modern instruments.

Those peoples for whom little is known regarding plant use are the Swazi, Transvaal Ndebele, Mpukushu (of the Okavango Delta) and the Khoi. The latter are, fortunately, now the subject of a research project by anthropologists at Stellenbosch University. The other three abovementioned cultural groups need considerable research. Continued recording of plant uses is, of course, also desirable for the other, better-studied, cultural groups. Projects at present being undertaken in Botswana and the northern coastal plain of Natal will greatly augment our knowledge of Tswana and Tonga plant utilization respectively.

Since research on folk taxonomy and plant-man interactions is precluded by the need to identify those plants that have uses, it is not surprising that so little work has been done on these two aspects thus far. The field is wide open and there is a lot of potential for research.

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Uses of graminaceous plants as food by man in West Africa

M. S. CHUAH*

ABSTRACT

The family Gramineae, with over 7 000 species is the fifth largest family in the plant kingdom, and has over the years played a very important role in providing food for man in the form of cereals among which the most important and well-known examples are rice, wheat, maize and others.

The principal graminaceous plants in man's diet in West Africa are rice (*Oryza* spp.); maize (*Zea mays* L.) and a variety of species belonging to the sorghums and millets (species of *Pennisetum, Digitaria* and *Eleusine*). Plants collected in times of famine include species of *Echinochloa, Panicum, Paspalum* etc.

RÉSUMÉ

UTILISATION DE PLANTES GRAMINÉENNES DANS L'ALIMENTATION DE L'HOMME EN AFRIQUE OCCIDENTALE

La famille des Gramineae, qui compte plus de 7 000 espèces, est la cinquième famille en importance du règne végétal et elle a, au cours des âges, joué un rôle très important dans l'approvisionnement alimentaire de l'homme sous forme de céréales parmi lesquelles les exemples les plus importants sont: le riz, le blé, le maïs et d'autres encore.

*Les graminées principales qui entrent dans l'alimentation humaine en Afrique occidentale sont: le riz (*Oryza *spp.); le maïs (*Zea mays *L.) et une variété d'espèces appartenant aux sorghos et millets (espèces de* Pennisetum, Digitaria *et* Eleusine). *Les plantes récoltées en temps de disette incluent espèces de* Echinochloa, Panicum *et* Paspalum etc.

The cereals are all members of the great grass family, Gramineae, and are alike in possessing the characteristic fruit of the family, the caryopsis. In this fruit the wall of the seed becomes fused with the ripening ovary wall to form the husk. The term 'grain' is also applied to this type of fruit.

The reasons for the importance of graminaceous plants as food plants are many. One or more of these grasses is available for each kind of climate. They have a wide range of soil and moisture requirements. They can be cultivated with a small amount of labour and have a high yield. The grains are high in food value and easy to handle and store because of their low water content. They contain a high percentage of carbohydrates, together with a considerable amount of proteins and some fat and vitamins.

The principal graminaceous plants in man's diet in West Africa are rice (*Oryza* spp.); maize (*Zea mays L.*) and a variety of species belonging to the sorghums and millets (species of *Pennisetum, Digitaria* and *Eleusine*). Several plants collected in times of famine include species of *Echinochloa, Panicum* and *Paspalum* etc.

These tropical African food plants follow a more or less strict climatic zonation. (Fig. 1). Above 10° latitude they form the basis of human food. South of the 1 000 isohyet the sorghums predominate; to the north they are slowly replaced by millet which is less demanding on water and practically disappears between the 400 and 600 isohyets.

In the intermediate zone between forest and savanna, rice and maize especially, play a large part in man's food, in association with tuberous plants, such as *Dioscorea* sp. *Manihot* sp. etc.

First in the list of West African food plants is *Zea mays* L. or maize as it is more commonly known. It is a native of tropical America and was introduced into West Africa in the sixteenth century. Maize is cultivated from the forest regions to the savanna areas. Two harvests are possible in forest regions, but one only in savanna areas during the rainy season. At harvest, a small proportion of the maize is eaten roasted, the rest turned into flour through the process of first drying the cobs, shelling the cobs, and then pounding the grains into flour or grinding in a mill. In this form, maize flour is used in the preparation of porridges.

Second on the list is *Oryza glaberrima* Steud., the indigenous African cultivated rice. It is grown on the flood plains from Senegal to Lake Chad. Nowhere in West Africa is this swamp rice specially irrigated as it is in many parts of the great rice growing countries of the East. The only irrigation done is natural irrigation, when the low-lying land in valleys becomes flooded in the rainy season and gradually dries off again after the rains have ceased.

Three main centres of origin of *Oryza glaberrima* Steud. exist: the first is in the Central Nigerian delta the second in Gambia and the third in Guinea (Fig. 2).

Preliminary attempts have been made to grow superior varieties of imported rice, *Oryza sativa* L. These varieties are better than local varieties in that they are heavy yielders and also do not shed their grain so easily during the period of harvest. Imported varieties thrive when the depth of water is regulated, but in West Africa where the irrigation of rice consists of natural flooding and the depth of water is very variable, the local varieties are much better suited to the sudden changes of water level.

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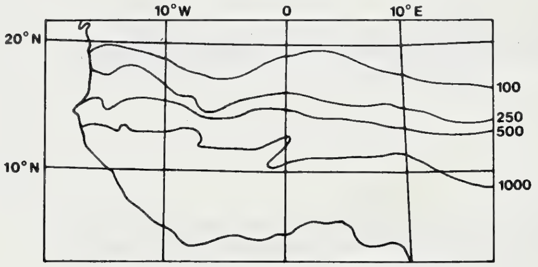

FIG. 1.—Mean annual rainfall in West Africa.

Two species of rice collected in the wild state include *Oryza barthii* A. Chev. and *O. breviligulata* A. Chev. & Roewr.

Third on the list are the sorghums which include a large number of widely cultivated grasses, known under a variety of names, common and scientific. Equatorial Africa is their native home. Although somewhat less nutritious than maize, they constitute a staple food for millions of native peoples in Africa especially in Senegal, Mali and Niger.

The plants are tall, coarse annuals; growing to a height of from 1–1,6 m and resembling maize in habit. The inflorescence is a dense head or panicle, and the grains are smaller and rounder than those of maize. The root system is shallow and twice as extensive as that of maize and the leaf area is half as great. The highly absorptive nature of the roots and the ability of the leaves to roll up in dry weather, enable the plants to withstand a great amount of heat and consequent evaporation. Their low water requirement renders them exceedingly drought resistant, so that they are well adapted to semi-arid and arid regions, where maize will not grow.

Sorghum bicolor (L.) Moench. is probably the commonest sorghum found in West Africa. All varieties are commonly used as food. It can be grown in districts with as low a rainfall as 30 or 50 cm per annum, but is generally found in those regions where the rainfall varies between 60–75 cm.

The main use of the *Sorghum* grains is as human food. The flour is generally mixed with water and made into foods resembling porridges. The seeds are also used in making intoxicating drinks.

Next we have the genus *Pennisetum.* Its species are well adapted to light soils and to drought and therefore is the main food of the most arid countries of tropical West Africa. The grains of *Pennisetum* are small and the term 'millet' is loosely applied to it and a large number of cultivated grasses with very small seeds. These grains are eaten in porridges, in making pancakes and in the making of fermented drinks.

Similar to the Pennisetums in having small seeds, are the Digitarias. Two species of major importance are *Digitaria iburua* Stapf and *D. exilis* (Kippist) Stapf. Their distribution is shown in Fig. 3.

The cultivation of *Digitaria iburua* Stapf is reduced to two regions, one on the Bauchi Plateau in North Nigeria, and the second in North Atacora (Togo-Benin) between 400–1 000 m asl. The

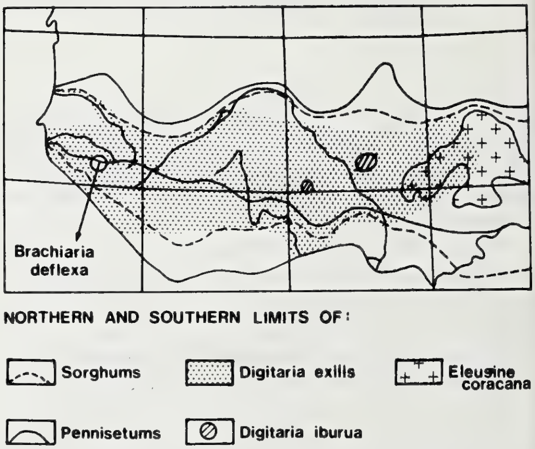

FIG. 3.—Northern and southern limits of the Sorghums, Pennisetums, *Digitaria exilis, D. iburua* and *Eleusine coracana.*

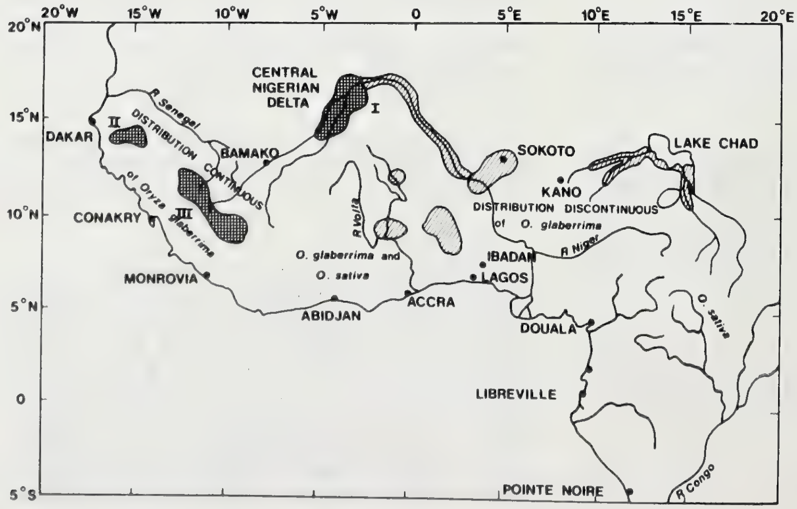

FIG. 2.—The distribution of *Oryza glaberrima* and its three centres of origin I, II & III in West Africa.

common name for *D. iburua* Stapf is iburua or black fonio. The grains are eaten as semolina by the Hausas. In Togo, they are used in making fermented drinks.

Digitaria exilis (Kippist) Stapf is the most important of the Digitarias. It is commonly known as fonio, fundi, acha or hungry rice. It is cultivated from Senegal to Chad. The grains have an agreeable taste, are easily digested and can be given to very young infants in the form of porridges. The common form in which it is eaten is semolina with meat, legume and other vegetables in sauce. The grains are also used in fermented drinks.

The following are graminaceous plants of minor importance as food. *Brachiaria deflexa* C. E. Hubb. is cultivated around Fouta Djalon in Mali (Fig. 3). In all other areas of West Africa it is collected in the wild. Its flour is used in making cakes.

Eleusine coracana Gaertn. is found in the region of Chad and Central African Republic. It is used as food for man and in the making of beers from coloured grains, whereas the white grains are used in making flour.

During famine or difficult periods the West African and the nomads resort to collecting the grains of the following graminaceous plants as food: *Brachiaria stigmatisata* Stapf., *Cenchrus biflorus* Roxb., *Dactyloctenium aegyptium* P. Beauv., *Digitaria adscendens* Henr., *Echinochloa colona* Link., *Eragrostis ciliaris* R. Br., *Panicum laetum* Kunth and *Paspalum scrobiculatum* L.

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Barrier plants in South Africa

L. HENDERSON*

ABSTRACT

It is stated that there is a need both to extend the range of barrier plants available in South Africa, and to replace some much-used exotic species that have become invasive. A literature survey and computerized herbarium search revealed that of the 428 plants recorded as having been used as barriers 62% are exotics. Of these, 26% are naturalized or invasive in one or other part of South Africa. Ideal characteristics for different types of barrier plants have been defined and used as a guide in selecting a range of potential barrier plants from the indigenous species available. Lists of recognized barrier plants are given including some species revealed as a result of the present investigation.

RÉSUMÉ

PLANTES POUR HAIES D'AFRIQUE DU SUD

Il est établi qu'il y a un besoin d'étendre la gamma des plantes pour haies disponibles en Afrique du Sud et de remplacer certaines espèces exotiques très utilisées qui sont devenues envahissantes. Un relevé de la litérature et une recherche en herbarium par ordinateur ont révélé que parmi les 428 plantes enregistrées comme ayant été utilisées comme haies, 62% sont exotiques. Parmi celles-ci 26% sont naturalisées ou envahissantes dans l'une ou l'autre partie de l'Afrique du Sud. Les caractéristiques idéales pour les différents types de plantes pour haies ont été définies et utilisées comme guide dans le choix d'une gamme de plantes pour haies potentielles à partir des espèces indigènes disponibles. Des listes de plantes pour haies connues sont fournies, incluant certaines espèces qui ont été reconnues à la suite de la présente investigation.

INTRODUCTION

Since the earliest times man has used plants to create physical barriers: as protection against wild animals and enemies; for shelter of dwellings, gardens, crops and livestock against injurious winds; to hide unsightly buildings or features of the environment; to provide privacy and for many other uses. Whereas in early times indigenous plants were used, the great majority of barrier plants in use in South Africa today are exotic.

There is a need to broaden the range of barrier plants available for various uses in different parts of South Africa. The different kinds of barrier plants needed include decorative hedges, windbreaks and security hedges. The environmental conditions where they are needed range from the deep soiled, humid coastal areas to the shallow soiled areas of the arid interior, where great temperature fluctuations are experienced.

In addition to the general need to extend the range of barrier plants available, there is a particular need to replace many of the exotic species presently in use, which have become invasive, threatening the pasture and tourist industries, and the indigenous flora. (Stirton, 1978).

As a first stage in meeting these needs, a literature and field survey has been undertaken to identify and characterize exotic and indigenous barrier plants that are currently in use, and indigenous species with potential as barrier plants.

LITERATURE SURVEY AND COMPUTER SEARCH OF NATIONAL HERBARIUM

No comprehensive study of barrier plants in South Africa has previously been undertaken, but substantial information is contained in 'Tree-planting in South Africa' (King, 1951), 'Characteristics and uses of trees and shrubs' (Poynton, 1972), and Department of Forestry guides to tree-planting and shelterbelts in South Africa (Fenn *et al.*, 1973; Haigh and Wilhelmij, 1973; Van Rensburg, 1973; Fenn *et al.*, 1974; Van Rensburg, 1975; Keet *et al.*, 1978; Van der Merwe *et al.*, 1978; and Wessels *et al.*, 1978). Other, less substantial, references are widely scattered in the literature, but in most cases these emphasize only the decorative qualities of the plants listed.

To add to the literature survey, a computer search was made of references to barrier plant usage on specimen labels in the National Herbarium, Pretoria.

CHARACTERIZATION OF BARRIER PLANTS AND FORMS OF USE

As an aid to analysis of the barrier plants available and those needed, the ideal physical, biological and horticultural characteristics of the various kinds of barrier plants were listed. Three major categories were considered: garden hedges, windbreaks/shelterbelts, and security hedges. Each of these is discussed below.

Garden hedges

These are primarily decorative barriers which may be clipped to form neat and attractive shapes. They are used to provide privacy or to partition areas within a garden.

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Physical characteristics
Growth form — woody shrubs and succulents
Morphology — multi-stemmed from the base or low-branching; dense foliage and closely arranged branchlets; should not be too thorny or difficult to clip.

Biological characteristics
Should respond well to cutting
Non-poisonous; non-irritant
Easy propagation and establishment by seed or vegetative means
Rapid growth; longevity/permanence
Disease and pest-free
Non-invasive

Horticultural characteristics
Attractive foliage, flowers and fruit

Windbreaks/shelterbelts

These serve primarily to break the force of winds, and to provide shelter to people, animals and farmsteads (shelterbelts) and orchards and crops (windbreaks).

Physical characteristics
Growth form — woody shrubs and trees
Morphology — low-branching and dense evergreen foliage; a minimum height of 5 m in most cases.

Biological characteristics
Tolerance to wind, and in coastal areas, to salt-spray
Easy propagation and establishment by seed or vegetative means
Rapid growth; longevity/permanence
Disease and pest-free
Non-invasive

Security hedges

These are primarily to prevent the passage of animals and people.

Physical characteristics
Growth form — woody or succulent shrubs or low-growing trees
Morphology — sturdy; multi-stemmed from the base or low-branching; dense branching; rigid or entangling branches; spreading crown; small sparsely distributed leaves that will cast little shade
Plant armature — spines, prickles, thorns.

Biological characteristics
Resistant to fire, trampling and browsing
Little attention or upkeep required after planting out
Capacity for regeneration if damaged
Ability to grow under a wide range of climatic and soil conditions
Irritant action through stinging hairs, latex or other means
Easy propagation and establishment by seed or vegetative means
Rapid growth; longevity/permanence
Disease and pest-free
Non-invasive

Combination of functions

On the outskirts of towns, and around farm gardens there is frequently a need for garden hedges to double as security hedges. For this purpose plants are required that combine decorative qualities with impenetrability.

Farmers also often like their shelterbelts to double as security fences, keeping the cattle in or out.

A useful measure of where the emphasis lies, is whether mixed plantings are acceptable or not. In garden hedges and sometimes in shelterbelts, uniformity is required and mixed plantings are unacceptable. In security hedges there are no such restrictions and any plant that contributes to the permanence and impenetrability of the barrier is welcome.

Combination plantings

Four categories have been used to classify the species needed for mixed plantings: framework plants, short fillers, tall fillers, and entanglers.

Framework plants are plants which will form the main framework of the barrier and ideally should have the aforementioned characteristics. It is unlikely, however, that they alone will form an impenetrable barrier and other plants will be required to fill in gaps and to strengthen the barrier.

Short fillers fill gaps between the ground and the lowermost branches of the framework plants. They should have many, rigid branches and be tolerant of shade.

Tall fillers fill gaps in and add height to the barrier. They should be much-branched but cast little shade.

Entanglers are plants which will thicken up the barriers as a whole and add to the difficulty of penetration. Suitable plants are prickly climbers which do not cast much shade.

RESULTS AND DISCUSSION

General analysis

The literature survey and computer search yielded the names of 428 plants used as barriers of various kinds in South Africa (Table 1). Of these, 294 (62%) are exotics, and 75 (26%) of the exotics are naturalized or invasive in some part of South Africa (Stirton, 1978; Wells *et al.*, 1980; Duggan & Henderson, 1981; and Balsinhas *et al.*, in press).

Exotic barrier plant species that are now pests in the country include:

(1) *Opuntia* species (Prickly pears), *Caesalpinia decapetala* (Mauritius thorn) which have been used as security barriers.

(2) *Leptospermum laevigatum* (Australian Myrtle), *Nerium oleander* (Oleander), *Hakea gibbosa* (Rock Hakea) and *Duranta repens* (Forget-me-not bush) which have been used as hedges.

(3) *Acacia saligna* (Port Jackson Willow), *Acacia cyclops* (Rooikrans), *Acacia longifolia* (long-leaved Wattle), *Acacia melanoxylon* (Blackwood), *Acacia*

TABLE 1.—The numbers of species that have been used or recommended for use in South Africa for the different barrier categories

Barrier category	Total no. of species	No. of indigenous species	% indigenous species
Garden hedges	253	96	38
Windbreaks/ shelterbelts	215	32	15
Security hedges	65	36	55
Combined categories	428	134	38

pycnantha (Golden Wattle), *Acacia dealbata* (Silver Wattle), *Acacia mearnsii* (Black Wattle) and *Pinus pinaster* (Cluster Pine) which have been used as windbreaks and shelterbelts.

Other plants, now accepted as indigenous, may owe their introduction and spread to their use as stockade plants e.g. *Euphorbia tirucalli* (Wells, 1959).

The use of exotics is especially prevalent in towns and cities where people have little knowledge of the potentials of indigenous plants and rely on plants readily available from nurserymen. Nurserymen, in turn have mainly confined their attention to well-known (tried and tested) exotic species.

There are other reasons for exotics being favoured. Firstly, there is a great demand for fast-growing, frost-hardy species for the cold interior regions of South Africa. These areas are very poor in indigenous woody species and at present the only species available of proven performance are exotic. Also, there has been very little serious investigation into the propagation, cultivation and utilization of indigenous plants (apart from the most showy ornamentals) and, finally, the public has been led to believe that our indigenous species are inferior to exotics.

In rural areas where people are in closer contact with the indigenous flora and where security hedges are more in demand than decorative hedges, there is a greater appreciation and use of indigenous species.

The use of some indigenous species for barrier purposes dates back to the earliest recorded history of South Africa. In those early days most barriers were planted for security reasons. Either live plants were used or the severed branches of spiny trees and shrubs were placed round kraals and fields. *Acacia karroo,* the sweet-thorn, was used extensively to make kraals for stock and even today it is often used for this purpose. The wolwedorings of the genus *Lycium* owe their common name to the fact that they once made spiny barriers round kraals to keep out hyaenas ('wolwe' or 'wolves' to the colonists). The spike-thorn, *Maytenus heterophylla,* the Kei-apple, *Dovyalis caffra* and the Buffalo thorn, *Ziziphus mucronata* have similar uses.

Garden hedges

Seven of the eleven most popular (the most quoted in the literature) exotic garden hedge species have become naturalized in parts of South Africa (Table 2). Five of these species, like some of our worst invasive exotic plants produce berries which are dispered by birds, thus adding to the problem of control.

Windbreaks/shelterbelts

Seven of the nineteen most popular (the most quoted in the literature) exotic species have become naturalized in parts of South Africa (Table 3). *Rhus lancea* is one of the very few indigenous species that is popularly used as a windbreak.

TABLE 2.—Indigenous and exotic garden hedge plants used in South Africa: the species most quoted in the literature

Indigenous species	Exotic species
Tecomaria capensis (Cape Honeysuckle)	*Hakea saligna* (Willow Hakea)*
Dodonaea viscosa (Sand Olive)	*Cotoneaster pannosa* (Cotoneaster)*†
Portulacaria afra (Spekboom)	*Ligustrum lucidum* (Chinese Privet)*†
Carissa macrocarpa (Amatungulu)	*Pyracantha coccinea* (Red-Firethorn)*†
Dovyalis caffra (Kei-apple)	*Ligustrum ibota* (Small-leaved Privet)†
Rhus lancea (Karree)	*Pyracantha angustifolia* (Yellow-Firethorn)*†
Pittosporum viridiflorum (Cape Pittosporum)	*Pyracantha coccinea* var. *lalandii* (Orange-Firethorn)†
Rhamnus prinoides (Glossy-leaf Redwood)	*Duranta repens* (Forget-me-not-bush)*
Plumbago capensis (Plumbago)	*Eugenia eucalyptoides* (Mimi)
Duvernoia adhatodoides (Pistol bush)	*Leptospermum laevigatum* (Australian Myrtle)*
Euphorbia tirucalli (Rubber hedge Euphorbia)	*Thuja orientalis* (Chinese Arbor-Vitae)
Myrsine africana (Cape Myrtle)	
Halleria lucida (Tree Fuschia)	

* Species which have become naturalized in parts of South Africa
† Exotic species which have bird-distributed berries

TABLE 3.—Indigenous and exotic windbreak/shelterbelt plants used in South Africa: the species most quoted in the literature

Indigenous species	Exotic species
Rhus lancea (Karree)	*Pinus halepensis* (Aleppo Pine)*
Podocarpus henkelii (Henkel's Yellowwood)	*Cedrus deodara* (Deodar)
Carissa macrocarpa (Amatungulu)	*Callitris glauca* (White Callitris)
Harpephyllum caffrum (Wild Plum)	*Ceratonia siliqua* (Carob)
Olea africana (Wild Olive)	*Pinus radiata* (Monterey Pine)*
Acacia karroo (Sweet thorn)	*Pinus roxburghii* (Chir Pine)
Chrysanthemoides monilifera (Bushtick berry)	*Acacia baileyana* (Bailey's Wattle)*
Podocarpus falcatus (Outeniqua Yellowwood)	*Cupressus sempervirens* var. *stricta* (Churchyard Cypress)
Rhus leptodictya (Mountain Karree)	*Eucalyptus melliodora* (Yellow Box)
Trichilia emetica (Natal Mahogany)	*Quercus ilex* (Holm Oak)
Virgilia oroboides (Keurboom)	*Acacia decurrens* (Green Wattle)*
	Casuarina cunninghamiana (Beefwood)
	Chamaecyparis lawsoniana (Lawson's Cypress)
	Eucalyptus camaldulensis (Red River Gum)
	Eucalyptus cinerea (Florist's Gum)*
	Eucalyptus sideroxylon (Black Ironbark)
	Pinus patula (Patula Pine)*
	Populus nigra var. *italica* (Lombardy Poplar)
	Schinus molle (Pepper tree)*

* Species which have become naturalized in parts of South Africa.

Security hedges

In the course of field surveys the writer has added 160 indigenous species to the list of species from the literature. Many of these plants may prove to be of limited use but at this stage they have been included because they possess one or more favourable characteristics. One hundred species have been assessed for their suitabilities in each of the security hedge plant categories and have been placed in high, medium and low priority classes.

All the high priority species (given in Table 4) have been selected from the northern parts of South Africa where the climatic conditions range from cold (with moderate frost) and dry to hot (frost-free) and dry and hot (frost-free) and moist.

TABLE 4.—Important security hedge plants identified from the literature and field investigations

Framework species	
Carissa macrocarpa (Amatungulu)	*Acacia erubescens* (Blue thorn)
Dovyalis caffra (Kei-apple)	*Acacia mellifera* (Black thorn)
Euphorbia grandicornis (Big-horned Euphorbia)	*Rhus ciliata* (Suur Karree)
Phoenix reclinata (Wild date palm)	*Euphorbia cooperi* (Lesser Candelabra tree)
Entada spicata (Spiny splinter bean)	*Dichrostachys cinerea* (Sickle bush)
Acacia schweinfurthii (River climbing Acacia)	*Acacia senegal* var. *rostrata* (Three-thorned Acacia)
Acacia ataxacantha (Flame Acacia)	*Terminalia prunioides* (Purple-pod Terminalia)
Acacia kraussiana (Coast climbing Acacia)	
Acacia luederitzii var. *retinens* (Bastard umbrella thorn)	
Short fillers	Tall fillers
Carissa bispinosa var. *bispinosa* (Num-Num)	*Balanites maughamii* (Torchwood)
Acacia hebeclada ssp. hebeclada (Candle-pod Acacia)	*Acacia senegal* var. *leiorachis* (Three-thorned Acacia)
Maytenus polyacantha (Kraal Spikethorn)	*Acacia nigrescens* (Knob-thorn)
Commiphora pyracanthoides (Common Commiphora)	
Entanglers	
Scutia myrtina (Cat-thorn)	*Asparagus racemosus* (Katbos)
Capparis sepiaria (Wild Caper bush)	*Asparagus saundersiae*
Capparis fascicularis	*Asparagus laricinus* (Katbos)
Smilax kraussiana	*Asparagus krebsianus*

Carissa macrocarpa and *Dovyalis caffra* are common hedge plants in South Africa. They are both extremely dense, spiny and sturdy. *D. caffra* is cultivated as a hedge and for its fruits as far afield as Australia, California and the Mediterranean countries.

The succulent Euphorbias have great potential as security barrier plants. Some species very closely resemble the 'ideal' framework species, being sturdy, drought resistant, armed with spines and having a milky latex which is toxic. In some species the latex is so toxic that it would serve as an immediate deterrent to any intruder. There is no other plant or group of plants either indigenous or exotic in South Africa that combines such formidable features. Disadvantages are that they are not fire-resistant, that they are difficult to handle, and that they are slow-growing. The latter disadvantage can be offset in some species by planting them as well-grown truncheons.

CONCLUSIONS

An analysis of the literature has confirmed that many exotic barrier plants are invasive and there is therefore a need for indigenous species to supplement and replace them. Initial field work has resulted in the identification of many potentially useful barrier plant species whose usefulness needs to be put to the test in a range of situations.

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Domestication of fynbos Proteaceae as a floricultural crop

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ABSTRACT

Domestication of a South African group of Proteaceae, the proteas, began with their cultivation as exotics in Europe. A growing local interest in their cultivation climaxed in the publication of a popular handbook in 1958. Commercial interest in cultivation and seed sources was stimulated and led to a botanical and horticultural survey of useful species throughout their distribution range in the fynbos. Information pamphlets on cultivation requirements and seed were eventually supplied to the public as an official service. Up to 1970 cut-flowers were harvested in limited quantities, mainly from the western Cape folded mountains, and sold on the European markets. During the last decade, the export trade in fresh Proteaceae flowers has become a significant factor in the national economy. However, the original system of harvesting from the natural habitat has caused serious marketing problems, for instance, poor cut-flower quality and an erratic supply of many species. Increased exploitation has also led to unprecedented disruptive pressure on the fynbos biome system, particularly on the Proteaceae-component. It is clear that the scientific cultivation of the protea family as a floricultural crop is necessary for its sustained growth as an economic factor, as well as for its natural conservation. The present paper gives an overview of the developments that led to the rise of the fynbos Proteaceae as a commercially cultivated crop in South Africa.

RÉSUMÉ

INTÉRÊT HORTICOLE DE L'ACCLIMATATION DES PROTEACÉES DU FYNBOS

L'acclimatation d'un groupe sud-africain de Protéacées les protéas débuta avec leur culture en tant que plantes exotiques en Europe. Un intérêt local croissant pour leur culture aboutit à la publication d'un manuel de vulgarisation en 1958. Un intérêt commercial dans la culture et les sources de semences fut stimulé et conduisit à un inventaire botanique et horticole des espèces utiles dans toute leur aire de repartition dans le fynbos. Des prospectus sur les exigences de leur culture et sur leur propagation furent finalement offerts au public à titre de service officiel. Jusqu'en 1970, les fleurs coupées furent récoltées en quantités limitées, surtout dans les montagnes plissées du Cap occidental, et vendues sur les marchés européens. Pendant la dernière décade, le marché d'exportation de fleurs fraiches de Protéacées est devenu un fracteur important dans l'économie nationale. Cependant le premier système de récolte, limité à l'habitat naturel, a causé de sérieux problèmes de commercialisation, par exemple la qualité médiocre des fleurs coupées et un approvisionnement irrégulier pour de nombreuses espèces. Une exploitation accrue a aussi amené une action perturbatrice sans précédent sur l'écosystème du fynbos, particulièrement sur sa composition en Protéacées. Il est clair qu'une exploration scientifique des Protéacées en horticulture est nécessaire tant pour maintenir le développement de ce fracteur économique, que pour protéger la famille à l'état naturel. Le présent document donne un aperçu des développements qui ont conduit les Protéacées du fynbos à devenir une culture pratiquée à une échelle commerciale en Afrique du Sud.

INTRODUCTION

The domestication of plants begins with cultivation. This is, in due course, followed by improvement of techniques and plant material (Jacobs, 1970). In modern society these functions are usually assigned to scientific research. The domestication of fynbos Proteaceae for horticultural use has been profoundly influenced by research contributions in their country of origin, South Africa.

CULTIVATION

The fynbos Proteaceae were first cultivated in Europe. An interest in the exotic plants from the Cape led to the cultivation of a number of species, under highly artificial conditions, during the late 18th and early 19th centuries (Rourke, 1980). However, the 'art' was soon lost, due to the lack of systematic knowledge of the requirements of these 'strange' plants. For the next 150 years, the only significant cultivation of the family, popularly known as proteas, was at the Cape; of special interest were the attempts, since 1913, by the National Botanic Gardens at Kirstenbosch (Vogts, 1962) and since about 1940, by two or three pioneering growers (Rourke, 1980). Their success was based partly on hit-or-miss methods and partly on study and observation of the natural habitat. However, all fynbos proteas cultivated with significant success were grown in the winter rainfall area, that is, in the region where they grow wild (Vogts, 1982).

RESEARCH

First phase

From approximately 1960, this limited scientific approach changed. The cultivation requirements of proteas were identified, classified and described in a popular handbook (Vogts, 1958). The information was drawn from the results of scientific experimentation, research and observation over a decade, of the behaviour of proteas cultivated outside their distribution range. This publication heralded the rapid establishment of protea cultivation and the intensification and expansion of research (Vogts, 1960; Letty, 1962; Rourke, 1980).

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The analysis of the basic cultural requirements of 52 species and 8 genera showed remarkable similarities within the family. Notwithstanding deviations in common needs, such as an alkaline soil required by some species instead of acid, it was generally accepted that all fynbos proteas could be considered for further investigation (Vogts, 1958).

The cultivation potential of proteas focused attention on their economic potential (Vogts, 1982). World-wide interest in the new and exotic in the cut-flower trade was indeed an impetus to bring these wild plants under human control.

At the same time, a breakthrough was achieved when South African proteas came on the European flower markets (Middelmann, 1981b). Most of these flowers were harvested directly from plants in the habitat. Hopes for the future of cultivation were, however, high and a 'South African Indigenous Flower Growers' Association' was formed in 1965 (Anonymous, 1965).

Conservation

The first serious problem which confronted the new phase of horticultural exploitation of proteas, was the protection of the natural sources of material. The exciting new interest in growing proteas for gain resulted in great numbers of prospective commercial growers harvesting plant material in the wild without the necessary know-how. Irreparable harm to rare plants, waste of seed collected at the wrong stage, and waste due to incorrect cultural methods soon led to a disastrous state of affairs. This was eventually brought under control, not so much by law enforcement, as by expert guidance (Vogts *et al.*, 1972) and by providing reproductive material (McCann, 1977; Anonymous, 1980). These official conservation actions were based on an awareness of the need to keep the natural resources intact (Vogts, 1982).

Reconnaissance survey of available resources: species, variants and ecotypes

It was realized by the authorities that, in order to cope with the growing interest in protea cultivation, an overall survey of the distribution area of the 300-odd species of Cape Proteaceae had to be undertaken (Nel, 1965). Localities in the south-western and southern Cape ranging from Clanwilliam to Grahamstown, were subsequently investigated systematically in different seasons from 1962 to 1972 (Vogts, 1972). All accessible and apparently suitable species were recorded as well as their habitats. Investigation of the latter included climatic data, elevation, aspect, soil analyses and associated plants (Vogts, 1972).

The most important contribution of this extensive survey project was the discovery of the variation of sub-populations within species. These were distinguishable from recognizable ecotypes with modified forms due to environmental conditions. These sub-populations were named commercial 'variants' (Vogts, 1980). A study of the variants of several species (up to the fourth generation) showed that many characteristics including flowering time of different populations of a species remain stable (Vogts, 1971; Vogts, 1980; Vogts, 1977c). It can be accepted that the discontinuous topography of the distribution area has contributed to bringing these variants to the threshold of speciation (Vogts, 1971). However, variants of some species may lose their distinguishing features in cultivation and revert back to the average, their characters obviously dependent on changeable environmental conditions. An example is the brilliant red of *Leucadendron salignum* from the Cold Bokkeveld (Vogts, 1980).

Evaluation and selection for further research

Over 150 species in their wild state proved to have some economic potential, 86 to a very high degree (Vogts, 1972). For practical reasons, only a few could be considered for intensive research. Those with the highest score of combined favourable characteristics were chosen.

Economic and horticultural potential was assessed on a number of points, of which the following were the most important (Vogts, 1980):

Attractive and arresting appearance, colour, shape and size of flowerhead; foliage attractive but not dominating,
Flowerhead not hidden or pendulous,
Erect growth providing good flowerstems,
Good cultivation potential and availability of propagation material,
Stability of characters,
Desired flowering times,
Postharvest quality,
No obnoxious odour.

Finally, about 14 species and a number of variants of the genera *Protea, Leucospermum, Leucadendron* and *Serruria* were selected for commercial cultivation. Examples are the red, summer-flowering variant of *Protea repens* (Vogts, 1980) and ten variants of *Protea cynaroides,* chosen to allow year-round production of flowers of this species (Vogts, 1977c).

Second phase

The above-mentioned pioneering research and publicity were prerequisites to the cultivation of proteas on a commercial level in South Africa. They also led to limited attempts at cultivation and research in other countries, for example in New Zealand (Brits, 1978a; Thomas, 1974). These activities, however, lacked a strong financial incentive, such as that engendered by the South African export trade (Brits, 1978a).

The next stage in the domestication of proteas, spanning the last decade, has been characterized by rapid developments. These were, firstly the exponential growth of the protea cut-flower export trade by an annual average of 20%, to a value of about R3 million in 1979/80. This growth created an industry of national economic significance (Strydom, 1980). Secondly, a concomitant and vigorous programme of basic and applied production research developed. In this period, commercial protea activity was also initiated in at least five other countries (Brits, 1978a; Middelmann, 1981a).

In South Africa, research continues to preceed the cultivation process in a curious way. An estimated 80% of all exported proteas are still being produced by the method of reaping directly from the habitat (veld-picking). This opportunistic practice is at variance with the principles of a sophisticated cut-flower marketing system and it may, in the long run, become counterproductive (Wood, 1980). The continuing disruption of the fynbos ecology, through selective commercial exploitation, also has serious ethical implications. The practice clearly conflicts with the growing concern in South Africa for conservation.

The considerable output of production research during the nineteen seventies has, therefore, been partly in anticipation of, and partly aimed at stimulating, cultivation (Strydom, 1978).

It is expected that the demands of increasing production costs, quality standards and competition will force ever-growing numbers of producers to resort to the cultivation of their product (Weiss, 1980; Strydom, 1980). It is believed that cultivated proteas may eventually replace the veld-picked product of the Western Cape to a large extent, if not completely.

The second research phase may be defined in terms of the problems which had to be overcome, in order to achieve the development of the protea family as a modern horticultural crop.

Seed dormancy in Leucospermum

Seed propagation of the genus *Leucospermum,* especially *L. cordifolium,* has always been difficult due to the severe dormancy exhibited by the seed (Brown & Van Staden, 1973; Brits, 1980d). Basic studies of the promotive effects of atmospheric oxygen in raising embryonic cytokinin levels (Van Staden & Brown, 1977), led to the development of a technique to break seed dormancy, consisting of imbibition in hydrogen peroxiue (Brits & Van Niekerk, 1976).

Vegetative propagation

Until as recently as 1974, all proteaceous plants were commercially propagated by seed. Seed propagation had all the inherent disadvantages of a heterozygous species. Techniques have now been developed to root selected protea clones on a large scale yielding vigorous, true-to-type plants with apparently normal root systems (Admiraal, 1966; Rousseau, 1966; Rousseau, 1967a; Jacobs & Steenkamp, 1975; Vogts, Rousseau & Blommaert, 1976). Although species of *Protea* are often difficult to root, members of the other commercial genera are generally easy to root, with indole butyric acid, under mistbed conditions (Jacobs & Steenkamp, 1976).

The dependency of many Proteaceae on low soil pH-values, their sensitivity to higher levels of soil solutes and the poor rooting ability of some clones prompted grafting research (Brits, 1978c). Species and clones suitable as rootstocks were identified and screened (Rousseau, 1967b; Z. Welgemoed, 1979b). In the genus *Leucospermum,* for example, the arborescent species *L. conocarpodendron* subsp. *conocarpodendron* and *L. patersonii,* proved to be the most suitable, as well as several vigorous hybrids which were tested as clonal rootstocks. A mass budding technique resulting in 95% success was developed, as well as an effective technique to graft onto the unrooted cuttings of a clonal rootstock, which are then rooted simultaneously with the process of graft wound healing (Z. Welgemoed, 1979b). These developments have placed the grafting of protea clones on a practical level comparable to the rooting of cuttings as a means of mass propagation.

Nutrition

The extreme sensitivity of the family to relatively moderate levels of phosphorus (Thomas, 1974; Claassens & Fölscher, 1978; Jones *et al.*, 1978) and the inability of most species to negotiate soil solutions in the higher pH-ranges (Vogts, 1958; Vogts, 1962) necessitated nutrition research. Some highly specific requirements have been identified, for example a preference of the family for nitrogen in the NH_4+-form and low levels of available potassium and phosphorus; proteas require nitrogen in relatively moderate amounts (Van Staden, 1968; Hanekom *et al.*, 1973; Claassens & Fölscher, 1978; Claassens, 1980).

Manipulation of growth habit

A study of the effects of ethephon and other growth regulators has revealed that it promoted lateral bud break of plants during vegetative flush. Tests on seedlings and rooted cuttings showed that early branching of both could be significantly increased by the application of ethephon as well as other feathering agents (Brits, 1977; Brits, 1980b). The same effect, though more costly, can be obtained by manual pruning (Vogts *et al.*, 1976a). This method is particularly useful in correcting the undesirable sprawling growth habit of many plants grown from terminal cuttings (Brits, 1980b).

Manipulation of flowering time in L. cordifolium

The main demand for imported cut-flowers on European markets falls within the South African midsummer. A basic problem of local *L. cordifolium* cut-flower production is the natural spring-flowering characteristic of the species (Brits, 1977).

The inflorescence of *Leucospermum* species is not borne terminally on a shoot, but in the axil of a leaf close to the shoot apex. Apart from this inflorescence referred to as the primary inflorescence, a number of axillary buds develop, situated immediately proximally to the primary inflorescence. These buds, referred to as secondary inflorescence buds, do not normally develop beyond the stage where they are 5 mm in diameter, due to correlative inhibition by the primary inflorescence. However, on removal of the primary inflorescence manually or chemically with ethephon sprays, one or sometimes more than one of the secondary inflorescence buds develop, giving rise to a secondary inflorescence which flowers later (Brits, 1977; Jacobs & Honeyborne, 1978). It has been shown that removal of the primary inflorescence of *Leucospermum* cv. 'Golden Star' on October 7 shifted the peak flowering period from October to December (Jacobs & Honeyborne, 1978). Secondary inflorescence buds may, however, abscise if the primary inflorescence is removed too late (Brits, 1977; Jacobs & Honeyborne, 1978). Flower initiation in *Leucospermum* has also been studied (Jacobs & Honeyborne, 1979; Jacobs & Minnaar, 1980a; Jacobs, 1980b).

Blackening of Protea *leaves*

The leaf colour of *Protea* cut-flowers air-shipped from South Africa to Europe, often undergoes a degenerative blackening during transit (Anonymous, 1965). This is unsightly and extremely damaging from the marketing point of view. Oxidation of flavonoids has been identified as one cause of the blackening in *Protea* leaves (Whitehead, 1979; De Swardt & Pretorius, 1980). High temperatures, low light intensity, desiccation and packing flowers with free water on the leaves all enhance blackening of the leaves (Jacobs & Minnaar, 1977a; Jacobs & Minnaar, 1977b; Jacobs & Minnaar, 1980b). Techniques of proper precooling have been developed as an efficient method of controlling leaf-blackening (Vogts *et al.*, 1976c; Jacobs 1980a; Jacobs, 1981).

Breeding

The breeding of superior protea types for horticulture was attempted on a limited scale before 1973 (Horn, 1962a; Horn, 1962b; Brits, 1980e).

In 1973 a mass selection programme of Proteaceae cutflower types was launched involving the scrutiny of most natural and cultivated resources of commercial Proteaceae in the Western Cape Province. Individual selections were indexed, established as vegetative clones and evaluated. The primary breeding goals established were cut-flower quality, variety, yield, ease of rooting and lateness of flowering. An interspecific hybridization programme was launched using the established selections of these proteas as the main contributors. A genetic investigation of interspecies crossing compatability was initiated (Brits, 1980b). Special techniques such as the polyploidization of proteas have been attempted (Van der Merwe, 1981).

Registration of protea cultivars

Prior to 1973, commercial resources were undescribed and were traded collectively under their old specific names, e.g. '*Leucospermum nutans*'. In 1973 a national cultivar registration programme for proteas was initiated (Brits, 1980c). In addition, authority was obtained from the ISHS (International Society for Horticultural Science) for South Africa to act as the International Registrar of all protea cultivars falling within the South African genera (Anonymous, 1975).

A first group of nine *Leucospermum*-selections and hybrids were registered as cut-flower cultivars and released, five in 1979 (Z. Welgemoed, 1979a; A. Welgemoed, 1979) and four in 1981 (Welgemoed, 1981; Anonymous 1981). *Protea repens:* Kouga variant, which was improved horticulturally by selection for deep red colour and early summer flowering time, was also released in 1981 (Welgemoed, 1981; Anonymous, 1981).

Diseases and pests of Proteaceae

Several studies have shown the Proteaceae to be exceptionally susceptible to the root-rot fungus *Phytophthora cinnamomi* Rands (Van Wyk, 1973a; Van Wyk, 1973b; Von Broembsen, 1981). A survey was conducted to determine the extent of *Phytophthora cinnamomi* infestation in protea nurseries and cut-flower plantations in the Western Cape (Von Broembsen, 1981). A sanitary programme was initiated to control the spread of the disease in nurseries, plantations and in the natural habitat. This included the publication and distribution of information pamphlets to producers (Brits & Von Broembsen, 1978). These measures form the basis of a long-term project to control *Phytophthora cinnamomi* on proteas in the Western Cape.

The commercial insect pests of proteas constitute a major problem field (Myburgh *et al.*, 1973). The problem is illustrated by the vast number of pests, estimated at more than 200 species (Gess, 1968) and probably more than the total number of pests of all introduced horticultural crops in the Western Cape. This is because proteas are cultivated within the boundaries of their natural habitat. A wide range of destructive insects has been identified (Myburgh *et al.*, 1973; Myburgh *et al.*, 1974; Myburgh & Rust, 1975) and efficient control measures for some have been developed (Myburgh *et al.*, 1976; Myburgh, 1978; Starke, 1979).

Communication between research and industry

The scattered distribution pattern of protea production areas in South Africa (Vogts, 1980) presents a considerable problem of communication. A protea information pamphlet series was initiated (Vogts, 1980; Vogts, *et al.*, 1976b; Jacobs & Steenkamp, 1975; Vogts *et al.*, 1976a; Vogts *et al.*, 1976c; Myburgh *et al.*, 1976; Brits & Von Broembsen, 1978; Jacobs & Steenkamp, 1976; Vogts, 1977a; Vogts 1977b; Vogts, 1977c; Starke, 1979; Vogts, 1979; De Swardt & Pretorius, 1980; Claassens, 1980). In addition, a mailing list of cut-flower producers was compiled on a national basis (Brits, 1978b). New information is regularly distributed free-of-charge to producers in South Africa as an extension service to the Industry.

CONCLUSION

The above is a summary of important problems and research contributions relating to protea culture in South Africa. The solution of these problems represents a significant advance in the domestication of the fynbos Proteaceae as a commercial flower crop.

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Annual habit and apomixis as drought adaptations in *Selaginella tenerrima*

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ABSTRACT

Selaginella tenerrima A. Braun ex Kuhn, widely distributed in the savanna-woodland and savanna zones of tropical Africa, is strictly annual. Dormant megaspores survive the yearly drought. Apomixis has been confirmed through laboratory cultures. Microsporangia are usually absent or very few, and the sporophyte chromosome number is triploid: 2n = 30.

RÉSUMÉ

LE CARACTÈRE ANNUEL ET L'APOMIXIE DE SELAGINELLA TENERRIMA: *FACTEURS D'ADAPTATION Á LA SÉCHERESSE*

Selaginella tenerrima *A. Braun ex Kuhn, largement répandue dans la savane boisée et les zones de savanes de l'Afrique tropicale, est strictement annuelle. Des mégaspores dormantes survivent aux sécheresses annuelles. L'apoximie a été confirmée par des cultures en laboratoire. Les microsporanges sont habituellement absents ou très limités et le nombre de chromosomes sporophytes est triploïde: 2n = 30.*

INTRODUCTION

The annual habit is very common in the angiosperms, especially those living under a seasonally dry climate. Such plants survive the rainless part of the year as dormant seeds, emerge during the rains, grow very rapidly, produce large quantities of seeds, and die away at the beginning of the next dry season. Similar life cycles (with the spores as drought surviving organs) are extremely rare in the pteridophytes, from among which only a few dwarfish selaginellas are unquestionably annuals. Until recently, very little was known about their biology.

Apomixis in the pteridophytes renders the reproduction independent of liquid water and considerably shortens the critical gametophytic phase. It has, therefore, often been regarded as an adaptation to xeric environments (Tryon, A. F., 1968; Klekowski, 1969). It is very rare within the genus *Selaginella,* and has up to the present been reported for only a few species, e.g. *S. rubricaulis* R. Sim and *S. spinulosa* A. Braun [= *S. selaginoides* (L.) Link] (Bruchmann, 1912), *S. anocardia* A. Braun (Goebel, 1915) and one race of *S. rupestris* (L.) Spring (Lyon, 1904; Tryon R. M., 1971). In all apomictic selaginellas microsporangia are very few or completely absent (Bower, 1935; Tryon R. M., 1955, 1971).

S. tenerrima A. Braun ex Kuhn from tropical Africa, combines both these remarkable features of annual habit and apomixis. A report on the seasonal pattern and reproductive biology of this species seems, therefore, to be of interest for students of pteridophyte ecology and evolution.

GEOGRAPHICAL DISTRIBUTION AND HABITAT REQUIREMENTS

S. tenerrima occurs in western, central and southern tropical Africa, from Guinea and Mali through Nigeria, Cameroon, the Central African Republic, Congo (Brazzaville) and Gabon to Angola, Zambia and Mozambique (Alston, 1957, 1959; Kornaś, 1979; Kuhn, 1868; Schelpe, 1970, 1977; Schelpe & Diniz, 1979; Tardieu-Blot, 1964a, 1964b). It certainly is much more widespread than indicated on our map (Fig. 1), but is very easily overlooked, because of its small size and moss-like appearance. It seems to be more common in the seasonally dry areas of the savanna-woodland and savanna zones, although a few stations in the rain forest zone (in S. Nigeria and Gabon) have also been recorded. It usually occurs in bare soil, forming small tufts, often associated with tiny bryophytes (e.g. *Fissidens* spp.), in rock crevices, under overhangs, around the bases of boulders in holes in the soil, and in other similar microhabitats, where it enjoys an increased humidity and some kind of protection from the competition of larger vascular plants.

PHENOLOGY AND LIFE-FORM

The seasonal pattern of growth and sporulation of *S. tenerrima* has been followed in two areas, one situated south of the equator, in Zambia, and the other north of the equator, in N.E. Nigeria and N. Cameroon. In both of them, young sporophytes emerged from the megaspores near the end of the rainy season: in April–June in Zambia and in September–November in Nigeria and Cameroon (Fig. 2). Germination of megaspores was apparently stimulated by the increase in soil moisture; laboratory experiments conducted in Poland have demonstrated, that the fresh megaspores from N. E. Nigeria were able to germinate in January and

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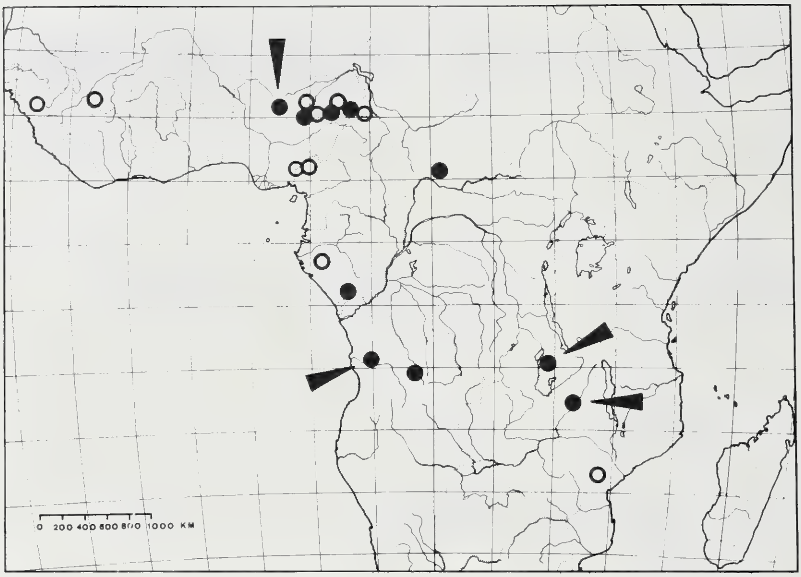

FIG. 1.—Distribution of *Selaginella tenerrima.* Solid circles show stations from which herbarium specimens have been revised, open circles represent records from literature. Stations from which microsporangia are known, are indicated by arrows.

February, therefore possibly lacking an inherent dormancy period. Sporophytes developed very fast under natural conditions and set strobili in a few weeks. In more humid habitats, they attained a height of up to 6 cm, but in the drier ones they remained dwarfish and often unbranched, forming a single strobilus at the apex of a stem of only 0,5 cm tall (Fig. 3).

The life duration of the sporophytes was extremely short. Soon after the end of the rains, they turned yellow and died. Megaspores were shed in such quantities that they were easily detectable on the soil surface near the tufts.

S. tenerrima is strictly annual: no perennating vegetative organs have ever been detected, and most of the mature sporophytes retained the empty wall of the megaspore at their base (Fig. 3).

REPRODUCTIVE BIOLOGY

All available living and herbarium material of *S. tenerrima* has been checked for the presence of strobili and the two types of sporangia (see Appendix). Practically every individual plant studied, even the smallest one, bore strobili, the number of which ranged from 1 to 40. Most of the sporophytes contained only megasporangia; in 5 samples (including the type collection from Angola — *Welwitsch* 45, BM, K) very few microsporangia were also seen (usually no more than 1–3 in c. 100 strobili inspected). The normal number of megaspores per sporangium was four, and their output in all populations was enormous — a feature which is similar to the very high production of seeds in annual angiosperms.

CULTURE EXPERIMENTS AND CHROMOSOME NUMBER

The populations of *S. tenerrima* studied in the field persisted from year to year even in the absence of microspores and microgametophytes. Apomixis is the only explanation of this situation. We were able to confirm this mode of reproduction in laboratory

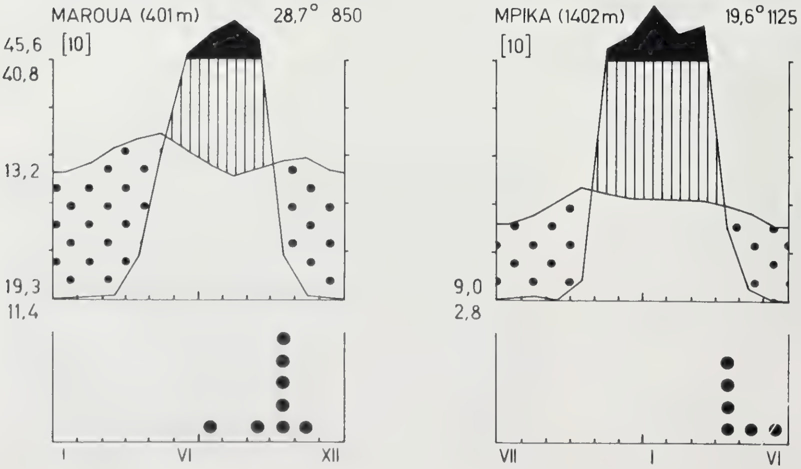

FIG. 2.—Above: climate diagram of stations in N. Cameroon (Maroua) and Zambia (Mpika) near which *Selaginella tenerrima* occurs. Drawn after Walter & Lieth (1960). Below: phenology of *S. tenerrima* in N.E. Nigeria and N. Cameroon (left) and in Zambia (right). Roman numerals designate the months; each dot shows one herbarium collection.

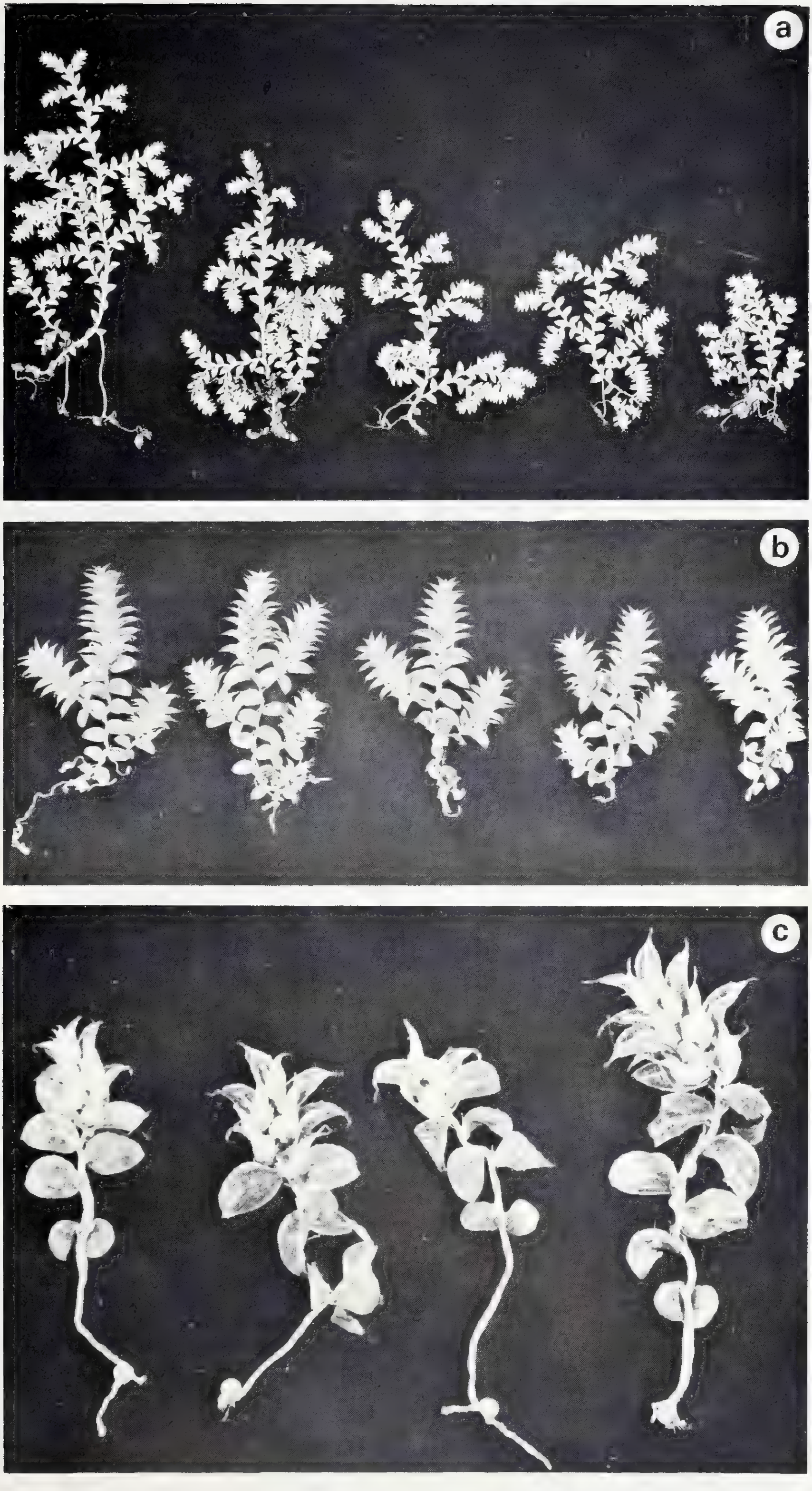

FIG. 3.—Sporophytes of *Selaginella tenerrima* from N.E. Nigeria, collected (a) in a very moist site under waterfall (*Kornaś* 6310) and (b, c) in a drier site in rock crevices (*Kornaś* 6214) (a, c. × 0,8; b, c. × 1,6; c, c. × 3,2).

cultures, where sporelings of up to six leaves were obtained from megaspores from three samples collected in N.E. Nigeria (*Kornaś* 6214, 6245, 6261 — see Appendix).

Megaspores are furnished with a trilete scar marking the commissures along which they dehisce. After a few weeks of watering, a germinating megaspore opened along the scar, expressing the prothallium with three tufts of rhizoids, which were twice as long as the diameter of the megaspore (Fig. 4). Such a quick germination is characteristic of tropical selaginellas as opposed to those of the temperate zones in which the dormant condition may last for many months or even for years (Bruchmann, 1912; Hofmeister, 1867). The prothallia of *S. tenerrima* never turned green, even on their tops. Several archegonia were formed on the upper surface of the prothallium. The short neck of each archegonium consisted of four rows of cells and was two cells high. Sporelings which grew in a permanent layer of water (1–2 mm) developed rhizoids which were visible up to the stage of two cotyledons, whereas sporelings growing in drier conditions were without rhizoids and had shorter hypocotyls (Figs 4 & 5).

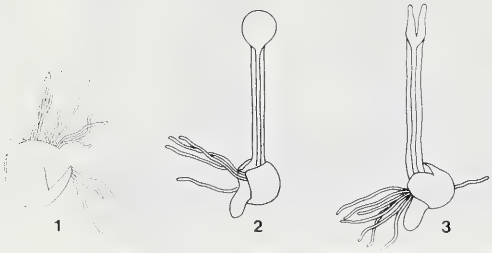

FIG. 4.—*Selaginella tenerrima* (*Kornaś* 6214). 1, dehiscent megaspore showing exposed prothallial tissue with rhizoids (c. × 15); 2 & 3, young sporelings (c. × 10).

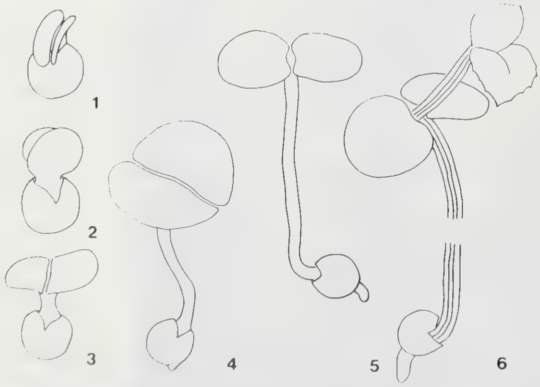

FIG. 5.—*Selaginella tenerrima* (*Kornaś* 6214). 1–6, young sporelings (c. × 10).

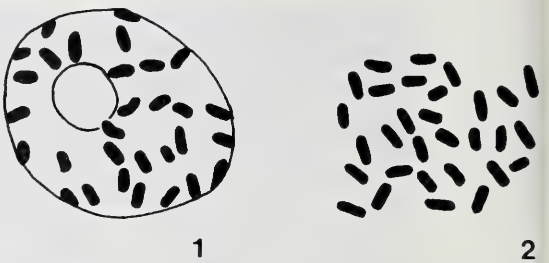

FIG. 6.—*Selaginella tenerrima* (*Kornaś* 6214). 2n = 30. 1, root tip prometaphase; 2, root-tip metaphase (c. × 4000).

Chromosome counts were made from root-tips and shoot apices of the sporelings. Material was fixed in Navashin's fixative diluted with an equal part of distilled water. Microtome sections 10 µm thick were stained with Newton's gentian violet. Chromosomes are small and have approximately the same length within the somatic plate (c. 0,7 µm). The chromosome number is 2n = 30 (Fig. 6).

The chromosome numbers in the genus *Selaginella* have been established for only c. 80 species out of the c. 700 known (Löve *et al.*, 1977). The basic numbers are x = 7, 8, 9 and 10. Therefore the investigated species *S. tenerrima* proved to be triploid. Unfortunately the mode of reproduction of the remaining triploid species (*S. bluuensis* v.A.v.R. from North Borneo, *S. biformis* A. Braun ex Kuhn and *S. vogelii* Spring from the Kew collection — Jermy *et al.*, 1967), is not known at present. Of the apomictic species, the chromosome numbers are known for *S. rupestris* (L.) Spring and *S. selaginoides* (L.) Link; they have both proved to be diploid with 2n = 18 (Löve *et al.*, 1977).

DISCUSSION

Annual selaginellas are currently known only from the tropic subtropic and south temperate regions of the Old World. Besides *S. tenerrima,* two other species have been reported to represent this life-form, namely *S. gracillima* (Kunze) Alston (= *S. preissiana* Spring) from Australia and *S. pygmaea* (Kaulf.) Alston [= *S. pumila* (Schlechtend.) Spring] from South Africa (Hieronymus, 1902; Velenovsky, 1905). In both species, empty megaspores are usually found attached to the base of mature sporophytes. Possibly a few other dwarfish selaginellas, closely resembling those listed above, have a similar life cycle, e.g. *S. ciliaris* (Retz.) Spring from S.E. Asia, N. Australia and W. Pacific, or *S. perpusilla* Baker from Africa and Madagascar. In *S. ciliaris,* apomixis seems to occur, as indicated by the lack of microsporangia (Alston, 1951; Hieronymus, 1902). Little is known about the habitat requirements of these tiny plants, but most probably they are similar to those of *S. tenerrima.* On the other hand, the annual selaginellas are included in various infrageneric taxa (*S. pygmaea* and *S. gracillima* in the subgenus *Homeophyllum, S. tenerrima* in the subgenus *Heterophyllum* — Hieronymus, 1902) and therefore their striking similarities may result rather from a convergent evolution, stimulated by the water stress in seasonally dry climates, than from a real phylogenetic affinity.

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APPENDIX: HERBARIUM SPECIMENS STUDIED

All specimens with megasporangia; micr. = microsporangia present.

NIGERIA.— Kaduna State: Samaru near Zaria, *Harris* et al. 7168 (KRA, micr.). Plateau State: Naraguta F. R., *Lawlor & Hall* FHI 46545 (K). Borno State: Gubi near Biu, *Kornaś* 6310 (KRA). Borno State: Takaskara Hills, *Kornaś* 6214 (KRA). Borno State: Ngoshe, *Kornaś* 6304 (KRA). Gongola State: Wuro Dawa, *Kornaś* 6261 (KRA). Gongola State: near Uba, *Kornaś* 6245 (KRA).

CAMEROON.—Koza, 20 km au N. de Mokolo, *Biholong* 120 (P).

CENTRAL AFRICAN REPUBLIC.—Rég. Bambari, Moroubas, *Tisserant* 2788 (P).

CONGO (BRAZZAVILLE).—Entre Sibité et Loudima, N. N. (P).

ANGOLA.—Distr. Golungo Alto, Serra do Alto Queta, *Welwitsch* 45 (BM; K, type collection; micr.). Lunda: Xá Sengue, *Exell & Mendonça* 402 (BM).

ZAMBIA.—Mporokoso Distr.: Lumangwe Falls, *Kornaś* 3748 (KRA, micr.), 3751 (KRA, micr.). Mpika Distr.: near Kapiri Kaswela, *Kornaś* 4024 (KRA, micr.).

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Interaction of ecology, taxonomy and distribution in some Mesembryanthemaceae

H. E. K. HARTMANN*

ABSTRACT

Many taxa of the family Mesembryanthemaceae show close correlations between distribution and environmental factors, e.g. occurrence on limestone or quartzite only, but few cases have been studied in detail. Recent investigations in anatomy, morphology, life cycles, physiology, and in energetic properties indicate that fundamentally different patterns are developed in adaptation to arid conditions, even in reaction to identical edaphic and climatic factors.

On the other hand, little is known about the immediate influence of changes in the natural environment. Studies in populations of the subgenus *Cephalophyllum* of the genus *Cephalophyllum* N.E. Br. show strong correlations between precipitation data and habit, which can superimpose genetic dispositions. In addition, growth forms are well adapted to certain types of plant communities, so that superficially, a diffuse structural pattern results.

Long term studies, in the field and in the greenhouse, of growth forms in relation to time, to precipitation, and to associations, allow first suggestions for adaptive pathways in the evolution of the group, and the results form a basis for taxonomic decisions in this highly confused taxon. Finally, the example offers aspects for the better understanding of interaction between ecology and distribution data.

RÉSUMÉ

INTERACTION DE L'ÉCOLOGIE, DE LA TAXONOMIE ET DE LA RÉPARTITION GÉOGRAPHIQUE CHEZ CERTAINES MÉSEMBRYANTHÉMACÉES

Beaucoup de taxons de la famille des Mésembryanthémacées montrent d'étroites correlations entre la répartition géographique et les facteurs du milieu, par exemple, leur présence seulement sur calcaire ou sur quartzite, mais peu de cas ont été étudiés en détail. De récentes investigations dans les domaines de l'anatomie, de la morphologie, des cycles biologiques, de la physiologie et des propriétés énergétiques indiquent que des modes fondamentalement différents d'adaption aux conditions arides se sont développés, même en réponse à des facteurs édaphiques et climatiques identiques.

D'autre part, on connaît peu de choses sur l'influence immédiate des changements dans le milieu naturel. Des études sur des populations du genre Cephalophyllum *N.E. Br., sous-genre* Cephalophyllum, *montrent de fortes corrélations entre les précipitations et le part qui peuvent déterminer des modifications génétiques. De plus, des formes biologiques sont bien adaptées à certains types de formations végétales, de sorte que superficiellement, il en résulte un mode de structure diffus.*

Des études à long terme, sur champ et en serre, des formes biologiques par rapport à la phénologie, aux précipitations et aux associations, permettent de formuler de premières hypothèses quant aux voies d'adaption suivies dans l'évolution du groupe; les résultats constituent une base pour le traitement systématique de ce taxon extrêmement confus. Finalement, cet exemple souligne la nécessité de mieux comprendre les rapports qui existent entre l'écologie et la repartition géographique.

INTRODUCTION

Members of the family Mesembryanthemaceae dominate wide areas in the drier parts of southern Africa, yet little information is available on the ecological requirements and exact distribution of species and even genera. This lack of knowledge is mainly due to insufficient taxonomic treatment, but adaptive strategies and population dynamics have also received little attention.

To illustrate the problem of possible interaction, the syndrome of runner formation in the genus *Cephalophyllum* has been studied as an example over five years, and first results allowing suggestions of evolutionary pathways are presented in this paper.

MATERIAL

Populations from the subgenus *Cephalophyllum* of the genus *Cephalophyllum* N.E.Br. have been chosen for the study for several reasons: the members of the subgenus are easy to identify by characters of fruit morphology, leaf shape, and growth form (described as '2. Gruppe' by Hartmann, 1978), they represent a well defined closely related complex; the delimination of species within the subgenus has been highly uncertain, because no critical evaluation of characters has been undertaken up to now; naming of species dates back to pre-Linnean times (e.g. Dillenius, 1732), but identification is extremely difficult because no types have been prepared, and only few drawings are available; and, finally, the distribution area of the group extends through different climatic regions, so that possible correlations with environmental factors can be examined. Although the taxonomic treatment of the subgenus has not yet been completed and a detailed monograph will be published later,

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the results allow the preliminary delimination of seven species, based on results of investigations into fruits, flowers, and leaves (for distribution of species see Fig. 1): *C. alstonii* Marloth ex L. Bol.; *C. corniculatum* (L.) Schw.; *C. diversiphyllum* (Haw.) H.E.K. Hartm. comb. nov. (Basionym: *Mesembryantheum diversiphyllum* Haw., Obs. Mesembr. 228, 1794; Lectotypus = iconotypus: t. 198, fig. 252 in: Dillenius, Hort. elth., 1732); *C. loreum* (L.) Schw.; *C. pillansii* L. Bol.; *C. purpureo-album* (Haw.) Schw.; and *C. tricolorum* (Haw.) Schw.

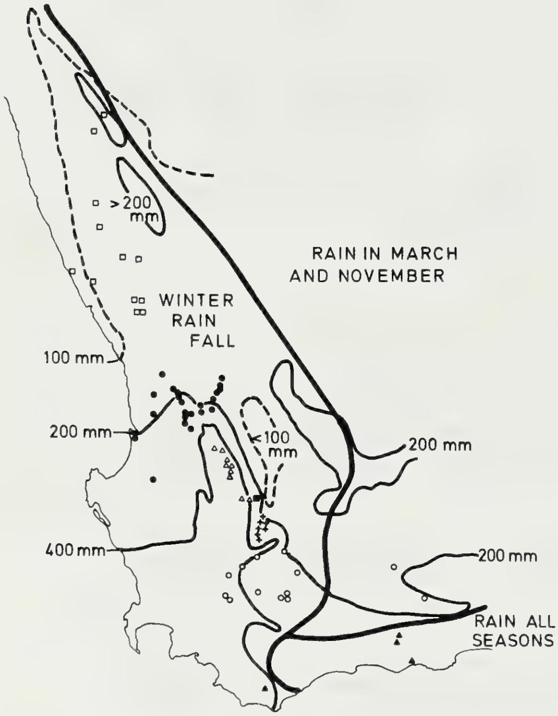

FIG. 1.—Geographical distribution of species of the subgenus *Cephalophyllum* of the genus *Cephalophyllum* N.E. Br. in relation to precipitation. For each species, the amount of rain expected per year is given in brackets; regional differences in rainfall are indicated on the map by thick continuous lines. Rainfall data after Schulze & McGee (1978) and monthly reports from the Weather Bureau, Pretoria. Full square: *C. alstonii* Marl. ex L. Bol. (± 200 mm); squares: *C. pillansii* L. Bol. (100–200 mm); crosses: *C. corniculatum* (L.) Schw. (200–400 mm); full circles: *C. tricolorum* (Haw.) Schw. (150–400 mm); circles: *C. purpureo-album* (Haw.) Schw. (<200 –> 400 mm); full triangles: *C. diversiphyllum* (Haw.) H.E.K. Hartm., comb. nov. (>200 mm); triangles: *C. loreum* (L.) Schw. (> 400 mm).

METHODS

Studies in growth forms in the genus *Cephalophyllum* (Hartmann, 1978) revealed that two fundamental types can be distinguished: flowers can occur in compound, dichotomous, annually-formed inflorescences (Fig. 2), or they can grow singly in leaf axils of long perennial axes (Fig. 3). In the first case, short runners are produced in order to bear the inflorescences. These die off at the end of the season and are replaced by new ones in the following year (Fig. 2). In the second case, runners persist for several years, they form several new internodes per year, and can reach considerable lengths (to 1 m), but branching is rare (Fig. 3). Intermediate stages exist and it was decided to use the length of runners and their number together with the number of seedlings established per population as parameters to examine development and stability of populations. To describe 'length of runners', the longest runner of each plant in the plot was measured in order to register the maximum potential per plant. From these measurements, the means of populations were calculated. 32 populations of five species of the subgenus *Cephalophyllum* were chosen out of 70 known ones. In small populations (n <100), all plants were recorded, whereas in larger ones representative plots were selected. The study was started in March 1977 — the dry season for most of the distribution area — and recording was repeated annually at about the same time of the year, until 1981. Final examinations are scheduled for February 1982. At least one plant of each population was transferred to greenhouses in Hamburg (Germany), mainly for studies of other characters, in order to achieve a taxonomic classification. Plants are kept at ± 10°C at night and 25–30°C during the day time, receiving additional light of about 5000 Lux for 10

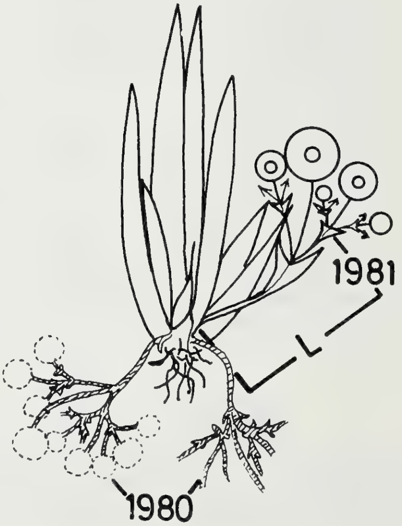

FIG. 2.—Plant with annual runners. 1980 = last year's inflorescences, 1981 = flowering inflorescence, L = length of runner.

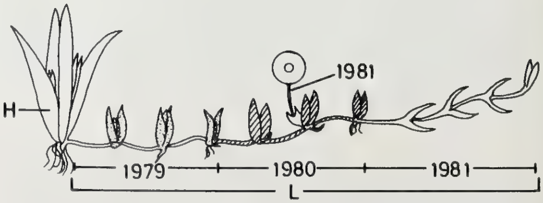

FIG. 3.—Plant with persistent runner; years of growth hatched differently. L = length of runner, H = head of plant.

hours per day. They are watered twice per week in winter, and once per month in summer, with gradual changes in spring and autumn.

ECOLOGY AND DISTRIBUTION OF SPECIES

It is known from other genera in the family Mesembryanthemaceae [e.g. *Odontophorus* N.E.Br. (Hartmann, 1976)] that infrageneric taxa can be correlated with distribution to rainfall patterns. Species of the subgenus *Cephalophyllum* show tendencies towards correlations of this type (Fig. 1), which include amount and seasonal distribution of rain as parameters.

Of particular interest is the distribution of *C. purpureo-album:* it occurs from areas where more than 400 mm annual precipitation is expected to regions with less than 200 mm of rain per year; in addition, rainfall can be registered in different seasons. In this species, leaf length has been found to be correlated with the amount of annual precipitation. The western populations develop longer and thicker leaves than the eastern ones, and an infraspecific cline is formed. The gradient of the ecocline is determined by the differences in amount of rainfall per year, irrespective of seasons.

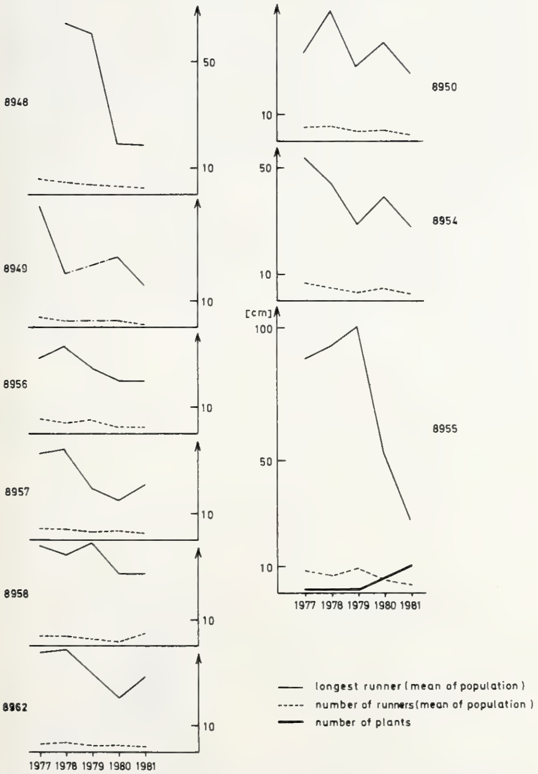

FIG. 4.—Annual changes in length and number of runners in *Cephalophyllum tricolorum* (Haw.) Schw. The ordinates represent both length in cm and number of runners; on the abscissa, the years are indicated. The figures at left are collecting numbers, one per population; populations are arranged in parallel north-south series from top to bottom, reflecting the geographic distribution. Each point on the curves represents the mean value per one year.

LONG TERM CHANGES IN RUNNER LENGTH AND NUMBER OF RUNNERS

Results of measurements and countings of runners over five years show distinct correlations to modes of runner formation, which will be discussed for each species.

In *C. tricolorum,* where persistent runners are developed, remarkable lengths have been measured (Fig. 4), but due to wide variation in values, no distinct limits can be given. Since the fluctuation in values does not concur simultaneously in all populations (compare e.g. 8954 and 8955, or 8957 and 8958 in Fig. 4), changes seem mainly to depend on local factors, and widespread influences can be excluded; dynamics of distinct populations will be discussed separately (section 6).

In *C. purpureo-album* (Fig. 5A) and *C. alstonii* (Fig. 5C), which develop annual runners as axes of inflorescences, the length seldom exceeds 10 cm, and consequently, variation is low. Similar values are found in *C. corniculatum* (Fig. 5D), a species with annual runners under favourable conditions, but these runners can become persistent and elongate in unfavourable situations.

In *C. loreum,* runner length shows a continuous increase from the northern to the central populations (Figs 1 & 5B), which is paralleled by an increased life span of runners in this series, thus presenting a geographic cline. The two south-eastern populations possess values closer to the centre of the cline. They cannot be linked up with the sequence.

The number of runners per plant can reach 10 in all species, but mean values per population rarely exceed 5. In general, it can be seen that an increase in the number of runners coincides with an increase in length of longest runners when mean values of populations are considered. In order to test the constancy of runner length and numbers, the mean values of populations per year are compared (Fig. 6). Although distinct centres can be identified in the diagram, it is also obvious that overlapping occurs. In general, it can be expected that annual runners (inflorescences) do not exceed 12 cm in length (open circles and squares in Fig. 6), whereas persistent runners reach 15 cm at least (dots in Fig. 6). The intermediate positions of *C. loreum* (L.) Schw. (triangles in Fig. 6) are discussed in section 7.

DYNAMICS OF POPULATIONS

Together with the recording of runners, the number of established seedlings was counted, and the general situation was observed. From these results, first insights into the dynamics of populations in arid habitats can be gained.

Most spectacular changes occur in the species *C. tricolorum* (Fig. 4), and, in addition, the development of a new population could be followed in this species (Table 1). The vigorous single plant was regarded as a fresh colonizer in 1977, because no dead remains of conspecific individuals were detected nearby, and the nearest living population of

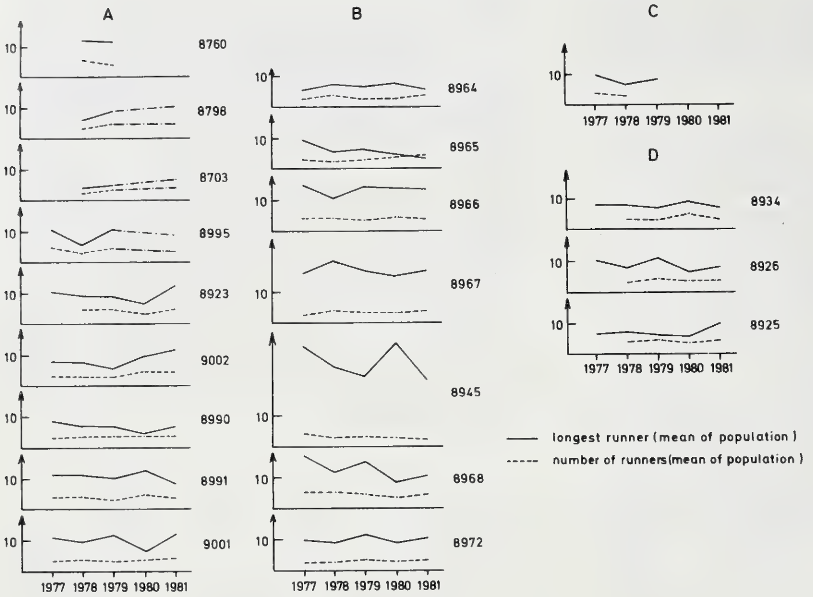

FIG. 5.—Annual changes in runner length and number. The figures at left are collection numbers, ordinates indicate numbers of runners and length (in cm) and points on the curves represent mean values per one year. A, *C. purpureo-album* (Haw.) Schw., the populations are arranged from east to west in the sequence from top to bottom, and can therefore be correlated to increasing amounts of rainfall per year (compare Fig. 1). B, *C. loreum* (L.) Schw., populations are arranged in north-south sequence from top to bottom, the top five ones representing a cline in increasing length of runners; C, *C. alstonii* Marl. ex L. Bol.; D, *C. corniculatum* (L.) Schw., populations are arranged in a north-south sequence from top to bottom.

the species was located 4 km away. No seedlings have been observed, although fruits have been formed. Instead, the plant developed side branches (Table 1, 1979), and the primary runners died away (Table 1, 1980), thus allowing secondary centres to develop into new plants (1980, 1981). In this case, the reduction in runner length (Fig. 4) is clearly correlated to an increase in number of plants (Table 1).

Similar models of dynamics can be seen in other populations of *C. tricolorum*, but causal factors can rarely be determined. An exception is presented by population *Hartmann* 8948, in which moles were reported in 1979, their activity resulting in a decrease of runner length in 1980 (Fig. 4, 8948). In general, it can be expected that populations of *C. tricolorum* in their young phases are composed of few large plants. An increase in number mainly seems to be reached by disintegration of long axes and the establishment of new plants from secondary heads (short side branches). Consequently, the initially high value for the longest runners of plants is reduced, while at the same time more individuals can be counted. Older populations often form an entangled mass of runners which can hardly be traced back to their origins. Although none of the observed populations has declined entirely, hardly any seedlings have been found either (35 out of 929 plants seen, i.e. about 3,5%). It might also be of importance to realize that these populations are genetically homogeneous, if they are derived from

TABLE 1.—Dynamics of a new population (*Hartmann* 8955)

Year	Number of plants	Number of runners	Length of longest runner (cm)	Notes
1977	1	8	88	—
1978	1	6	93	—
1979	1	9	100	long runners with side branches
1980	5	5 5 3 3 6	30 84 30 16 102 $\overline{x}$ = 52,4	original runners dying out, new ones forming from secondary centres
1981	10	? 2 1 7 3 1 2 2 1 4	62 27 20 38 15 15 17 22 20 33 $\overline{x}$ = 26,9	

Note: values of numbers of runners and length of longest runner for 1980 and 1981 are arranged in such a way that corresponding positions refer to the same plant.

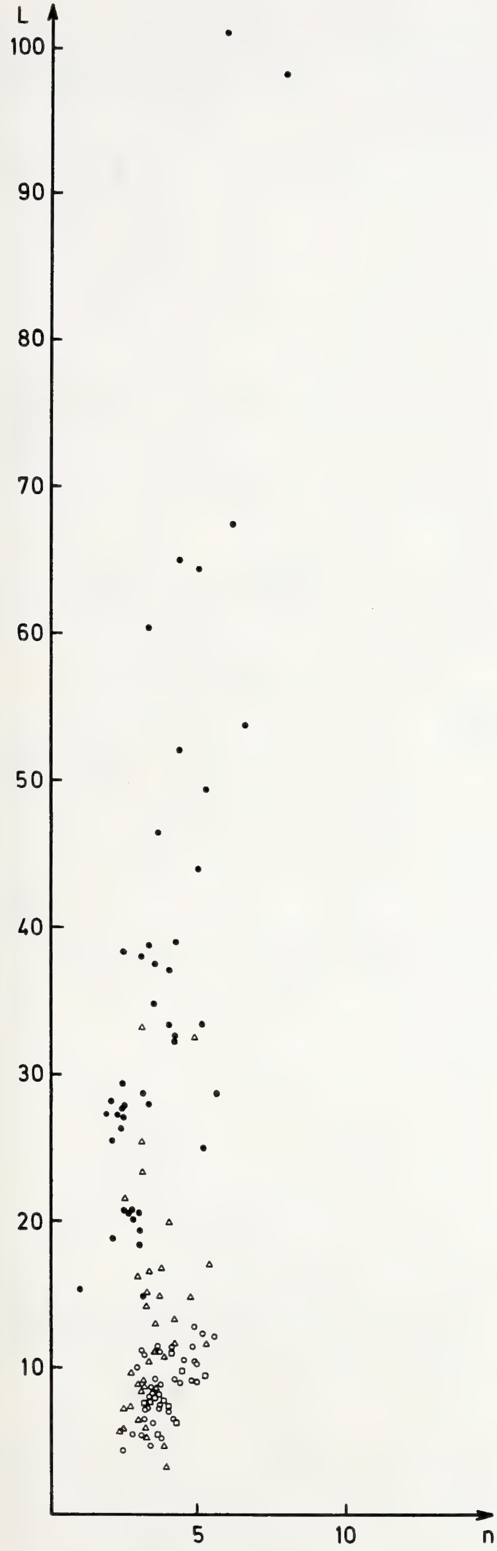

FIG. 6.—Comparison of runner length (L in cm) and runner number (n) of different species. Full square: *C. alstonii* Marl. ex L. Bol.; triangles: *C. loreum* (L.) Schw.; circles: *C. purpureo-album* (Haw.) Schw.; full circles: *C. tricolorum* (Haw.) Schw. Each symbol represents the mean value of one population in one year.

one single plant, like *Hartmann* 8955. Furthermore, it should be noted that flowering is not abundant in the species, and even further reduced in greenhouse cultures.

In the species *C. purpureo-album* (Fig. 5A), *C. alstonii* (Fig. 5C) and *C. corniculatum* (Fig 5D), little variation in length of longest runners has been found. The limited growth can be interpreted as an economic adaptation, because the runners are only used during a single season. Thus, the loss of material is kept low.

In *C. purpureo-album,* a particularly high rate of germination and establishment of seedlings has been observed: young plants without runners can amount to 60% of a population. Mean values for seedlings over five years exceed 10% in general. Since hardly any vegetative reproduction occurs, a high rate of germination is required to keep the species in existence. The life span that plants of *C. purpureo-album* can reach under natural conditions, in comparison with plants of *C. tricolorum,* has not yet been investigated. Plants of both species have been kept in culture for seven years now without showing signs of decline.

Three populations of *C. corniculatum* have been recorded, between which the proportion of seedlings varies widely (*Hartmann* 8925: 4%, n = 143; *Hartmann* 8926: 26%, n = 339; *Hartmann* 8934: 5%, n = 184), and shows no correlation at all to lengths of runners (compare Fig. 5D).

Of *C. alstonii,* only one small population is known, in which the number of plants varied from 15 to 11 during the investigation. It was impossible to identify seedlings, because the population was in poor condition and adult plants without runners existed. The possibility cannot be excluded that fruits and plants are removed by collectors, since the species is considered particularly interesting by amateur growers in Europe.

Like *C. corniculatum, C. loreum* varies considerably in proportions of seedlings but, in the last-named species, the percentage of seedlings of a population is correlated to the prevailing length of longest runners in that population (Table 2 and Fig. 5B): the more seedlings that are established, the more shorter runners can be expected in the adult plants.

The example of *C. loreum* stresses the fact that dynamics of populations can follow either strategy: if little material is invested into vegetative parts (short runners), many seedlings are established under normal natural conditions (10–60% in one population); if much material is used for production of vegetative parts (long runners), less is invested into sexual reproduction and only few seedlings are developed (3–5%).

POPULATION DYNAMICS IN RELATION TO CLIMATIC CHANGES

The composition of population has been shown to vary from year to year, a process which can be expected to depend on climatic factors. For a first

TABLE 2.—Correlation between length of runners and proportion of seedlings in *Cephylophyllum loreum*

Collection number (*Hartmann*) arranged in N–S-sequence	Length of runners (highest annual means in cm)	Seedlings in % over five years
8964	8,74	26,15
8965	9,18	10,74
8966	14,90	3,19
8967	20,00	8,07
8945	33,68	4,55
8968*	17,00	12,60
8972*	11,00	9,70

* Geographically separated populations.

test, amount and frequencies of rainfall have been analysed and correlated with one another.

One population of *C. purpureo-album* (*Hartmann* 9001) grows near Worcester in the Cape, from where precipitation data on a monthly basis are available. Comparison of data indicates, that the amount of rain in one year is correlated to the number of established seedlings in March/April of the following year (Fig. 7). It is suggested that the rate of reproduction by seeds in this population is directly influenced by the available moisture. Closer investigation (Fig. 8) into the seasonal distribution of rainfall reveals even more limited correlation factors: rains occurring out of season, like the summer rains in January and February 1979, do not result in an increased number of seedlings as counted in March 1979. Obviously, only winter rain allows the germination and subsequent growth of seedlings, whereas at the same time the amount of this rain determines the number of seedlings per population. On the other hand, no influence of rainfall on length or number of runners has been detected, although the fact of annual runner production suggests possible interrelations (Fig. 7).

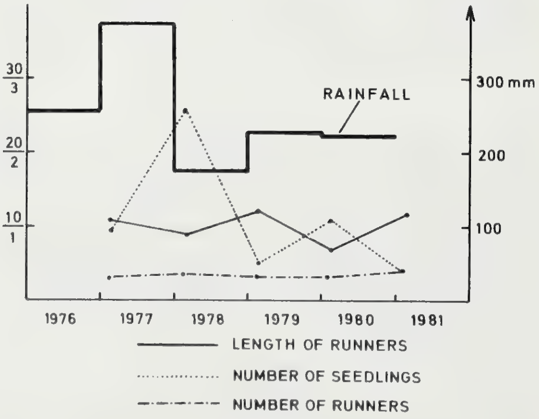

FIG. 7.—Dynamics of one population in relation to precipitation (*Hartmann* 9001). Amount of annual precipitation (in mm) = thick continuous line. Number of seedlings = dotted line; number of runners = broken dotted line; length of runners (in cm) = thin continuous line.

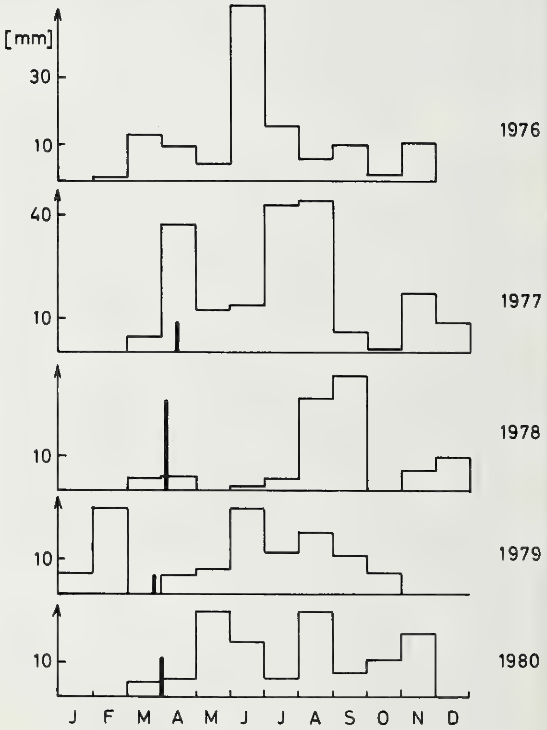

FIG. 8.—Monthly pattern of rainfall at Worcester, near population *Hartmann* 9001. The number of seedlings counted in March is indicated by a vertical line and can be correlated with the amount of rainfall: abundant winter rains result in high proportions of established seedlings. Note the missing correlation between summer rain and number of seedlings in early 1979.

It should be of interest to analyse analogous correlations in the species *C. tricolorum* with persistent runners, but up to now no locality has been found from where precipitation data and the existence of a population are known.

In the absence of rainfall data, associations of plants could serve as indicators for climatic factors, but information in this field is extremely limited. Preliminary notes on associations in which the populations of *C. loreum* occur, indicate close correlations between runner formation and flora: plants with shortest runners (Fig. 5B) grow in the most northerly locality together with ericaceous and restionaceous elements, probably a typical fynbos association. Following the series of populations further to the south, more succulent elements occur and the number of fynbos associates is reduced and, at the same time, the length of runners increases considerably (Table 2 and Fig. 5B). The change is probably determined by differences in precipitation, the most northern population representing the highest localities inhabitable by the genus, and receiving relatively high amounts of rain. Towards the south, the localities are situated at lower altitudes and receive less rain (Taylor, 1978), since they are sheltered from west rains by the Cedar Mountains and the Koue Bokkeveld Mountains. Therefore, in the centre of the series, *Elytropappus rhinocerotis* (Renosterbos) is dominant whereas towards the south succulent shrubs increase in proportion.

Further detailed investigations into the associations and the tentative correlations to length of runners and seedling establishment are scheduled.

DISCUSSION AND CONCLUSIONS

The results permit a preliminary understanding of mechanisms that govern the distribution of taxa via ecological factors. It is clearly shown that species of one genus can exhibit marked differences in population dynamics. In this case, two dispersal strategies can be emphasized alternatively, the alternatives being reduced to survival mechanisms under extreme unfavourable conditions in each respective group. Changes in populations can be influenced by amount and time of rainfall through the establishment of seedlings, yet no general adaptive trend can be recognized within the group. The distribution map (Fig. 1) clearly shows that growth forms with short annual runners occur in the regions with low precipitation (*C. pillansii,* 100–200 mm of rain per year) as well as in areas where higher rainfalls are expected (*C. purpureo-album,* up to 400 mm annual precipitation). Therefore it seems unlikely that either of the extreme growth forms can be considered to represent an original stage. Rather, it can be assumed that a putative ancestor possessed ambivalent potentials, which were realized depending upon prevailing conditions. It is suggested that the constant extremes have evolved from an ancient stock with variable growth forms and that fixing of genetic pattern has taken place. Consequently, species with a single growth and reproduction type are seen as final stages in evolutionary lines, and *C. pillansii, C. tricolorum, C. purpureo-album* and *C. alstonii* as highest evolved species. In contrast, the instability in growth form and reproduction types indicate that in *C. loreum* and *C. corniculatum,* primitive features of the group have been preserved. If these interpretations are correct, the evolution of the group probably started in associations bordering fynbos and receiving less than 250 mm of annual precipitation. Depending on the extension of suitable areas in different geological times, the total region inhabited by the subgenus might have been much greater, and the restricted distribution found today may represent the result of retreats.

It must remain open at this stage of investigation whether the assumed processes reflect similar evolutionary lines for the entire family. Certainly, the conclusions agree with results from anatomical studies of leaf surfaces (Ihlenfeldt & Hartmann, in press), which place the genus *Cephalophyllum* between xeromorphic and non-xeromorphic surface types, evolution being supposed to have developed from non-xeromorphic types.

Finally, it seems important to realize that different types of population dynamics can be correlated to different taxa, thus presenting a set of characters of considerable potential for taxonomic conclusions.

ACKNOWLEDGEMENTS

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Dune vegetation dynamics from 1937 to 1976 in the Mlalazi-Richards Bay area of Natal, South Africa

P. J. WEISSER* and R. MÜLLER*

ABSTRACT

Dune vegetation changes were studied qualitatively with the aid of air photos taken in 1937, 1957 and 1976. Results were transferred to 1:10 000 scale maps. In 1937 roughly 80% of the dune forest habitat was occupied by planted fields and post cultivation seral stages such as Secondary Grasslands and Dwarf Shrubland, Secondary Scrub and *Acacia karroo* Woodland. In three areas, the vegetation cover had been completely destroyed and drift sands had formed. In the 1950's the trend of vegetation degradation was changed by the implementation of an afforestation programme by the Department of Forestry. The 1976 air photos indicate that the post cultivation seral stages of 1937 had been largely replaced by forest plantations. In secondary, unafforested areas the vegetation is evolving rapidly towards a Secondary Dune Forest.

RÉSUMÉ

DYNAMIQUE DE LA VÉGÉTATION DES DUNES DE 1937 À 1976 DANS LA RÉGION DE MLALAZI-RICHARDS BAY AU NATAL, AFRIQUE DU SUD

Les changements dans la végétation des dunes ont été étudiés qualitativement à l'aide de photographies aériennes prises en 1937, 1957 et 1976. Les résultats furent reportés sur des cartes à l'échelle de 1:10 000. En 1937, approximativement 80% de l'habitat des forêts de dunes étaient occupés par des champs cultivés et des stades d'évolution post-culturale tels que des formations herbeuses secondaires et une formation arbustive naine, une formation broussailleuse secondaires et une forêt claire à Acacia karroo. *Dans trois régions, la couverture végétale était détruite et des dunes mobiles s'étaient formées. Dans les années 50, le tendance vers une dégrádation de la végétation se modifia par la mise en oeuvre d'un programme de reboisement par le Département des forêts. Les photographies aériennes de 1976 indiquent que les stades d'évolution post-culturale de 1937 avaient été, pour la plupart, remplacés par des plantations forestières. Dans les zones secondaires, non reboisées, la végétation évolue rapidement vers une forêt de dune secondaire.*

INTRODUCTION

Huntley (1977), in reviewing terrestrial ecology in South Africa, indicated that whereas considerable progress had been made in mapping our country's vegetation, little effort had been made to obtain information on vegetation trends. This work aims to provide information in this field.

The objectives of this study of the Mlalazi-Richards Bay area of Natal were: (1) to provide an inventory of mapping units as determined from air photos; (2) to produce 1:10 000 vegetation maps that could serve for management and vegetation monitoring purposes; and (3) to study vegetation changes and their causes, by using historic photos taken in 1937 and 1957.

Aerial photography has been used before to show qualitative changes and trends in coast-dune and estuarine ecology in the Natal coastal region (Ward, 1971 *vide* Edwards, 1972) and Weisser & Marques (1979).

STUDY AREA

The coastal zone between Richards Bay Sanctuary and Mlalazi Estuary is a vegetated strip of dunes 28 km long, on the Natal Coast between 28°50′ and 28°57½′ South and 31°46½′ and 32°03′ East (Fig. 1). The maximum width of the dune field is 2 250 m, averaging about 1 500 m and the area covers about 3 300 ha. The highest dune reaches 79 m above sea level.

The coastal dune soils (*vide* Venter, 1972) are predominantly sandy, and the climate is humid and warm to hot with a high year-round rainfall (Schulze, 1965). The mean annual temperature at the Cape St Lucia Station is 21,5°C and the mean annual rainfall at the Umhlatuzi Valley Sugar Estates near Richards Bay is 1 106 mm (Venter, 1972). Prevailing winds are NE and SW. Plant growth is luxuriant and tropical. The region falls within the 20°C isotherm, which is accepted as the limit for tropical vegetation (Aubert de la Rue *et al.*, 1958, in Venter, *l.c.).*

This dune area was part of Reserve 10, which was reallocated in 1952 to the Forestry Department under the Bantu Trust and Land Act, and handed over to Kwazulu on 1972-04-01 (Bower, MS.). Today the area falls under the jurisdiction of the Agriculture and Forestry Department of Kwazulu.

METHODS AND MATERIALS

Air photos were chosen as the main source of information as adequate material was available dating as far back as 1937. Mapping of the vegetation was done from air photos of Job 117–37 (1937, Trigonometrical Survey, Pretoria) and Job 251, University of Natal (1976) through direct inspection, enlargement and transference onto base maps using a Bausch & Lomb ZT–4 Zoom Transfer Scope (ZTS). This instrument was also employed to draw the six base maps from ortho-photo maps. As no ortho-photo map was available at the time for the

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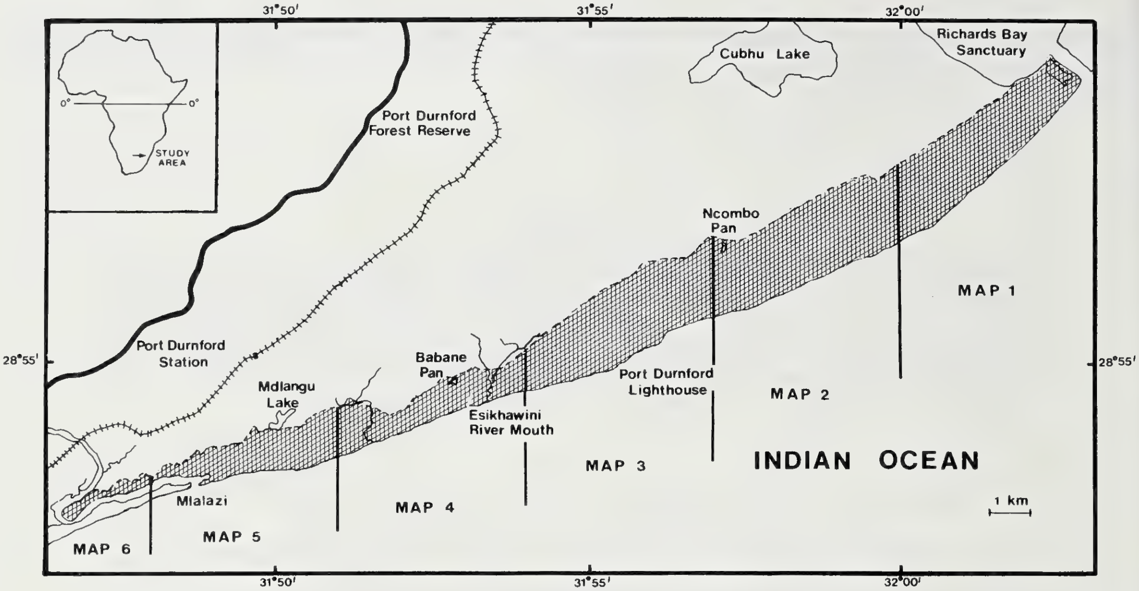

FIG. 1.—Location of study area (hatched) showing areas covered by the six maps.

Mlalazi Peninsula, the base map for that area was drawn directly from air photos. Fig. 1 indicates the area covered by each map. Interpretation of the aerial photographs was aided by a Topcon Stereoscope. Areas were measured with a MOP–AM02 Image Analyser. Ground truth and additional field data were gathered during 1979–1981.

Mapping units were based on air-photo interpretation and available field information. The 1937 vegetation maps were taken as the base line from which to monitor changes.

The photos used in the study were of different scales, varied quality and were taken under different conditions. No field data are available for checking the interpretation of the photos of 1937. These factors make comparison between different sets of air photos difficult. The advantages and disadvantages of the use of air photos for vegetation studies has been reviewed by Edwards (1972) and Weisser (1979).

Because of air photo distortion, the positioning of vegetation patches on the maps is only approximate. The air photos were realigned as soon as a deviation of corresponding points and areas was observed, while mapping was being done.

RESULTS

Mapping units, inventory and vegetation trends

Fifteen mapping units were identified by air-photo interpretation. A short description of them, their location, the trends observed and the inferred future development for the main mapping units follows. A more detailed description of the mapping units, and quantification of the vegetation changes is in preparation (Weisser, MS.). Additional information on the vegetation of the Richards Bay section of the study area is provided by Venter (1972).

1. *Beach*

In this mapping unit, the interface between sea and dunes was mapped. Interrupted by only two rocky outcrops, it forms an almost continuous band between the Richards Bay Sanctuary Mouth and Mlalazi Estuary. Dune pioneer communities may occasionally have been included in this unit, where they were masked by reflection from the beach sand.

Air-photo interpretation and field inspection showed one coastal erosion zone with narrow beaches and slumping dunefront (Fig. 2) in between two sand accretion zones with wide beaches. The first sand accretion zone extends from Richards Bay Sanctuary Mouth to about 4 km south and the second extends from Mlalazi Estuary northwards for about 4,5 km, whereas the retreating coast lies between these areas.

The greatest accretion was found north of the Mlalazi Estuary, where the beach advanced about 70 metres from 1937 to 1976. This sand accumulation could be related to agricultural malpractices in the catchment area that lead to an increase of sediments brought to the sea by the Tugela and Mlalazi Rivers.

2. *Littoral drift sands*

Drift sands that originate on the beach form tongues into the vegetated dunes. Keet (1936) and Stephens (1939) maintain that many drift sands start as cattle paths which expose the sand to the wind after the vegetation has been destroyed. Many drift sands were too small to be mapped, because their size was less than the mapping resolution. The position of the drift sands was reasonably constant through the years along the coast, and they often provided useful matching points during mapping.

By comparing 1937 and 1976 maps, a reduction in size and number of coastal drift sands was found.

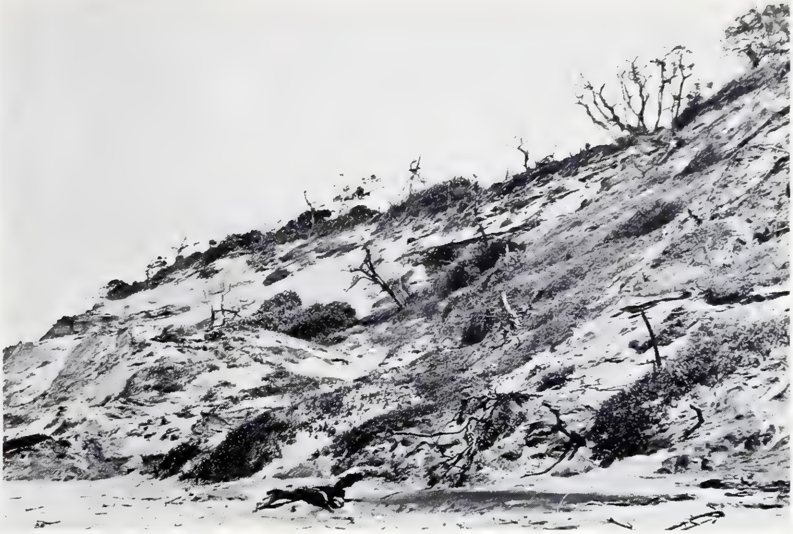

FIG. 2.—Undercutting by the sea and slumping of dune barrier is common. Pioneer communities frequently establish themselves on newly exposed surfaces (January, 1979).

This was probably a consequence of the protective management (e.g. reduction of grazing and fire) carried out by the Department of Forestry and of their drift sand rehabilitation programme using *Casuarina equisetifolia.*

3. *Inland drift sands*

Three main inland drift sands were found on the 1937 photographs. On the 1976 photos they were found to have stabilized mainly through the plantings of *Casuarina equisetifolia* (Fig. 5).

Under present management, there is no danger of drift sands recurring. However, their presence in 1937 is a warning of the potential dangers inherent in the abuse of the area.

4. *Sand and clay quarries*

These bare areas have arisen because of quarrying activities.

5. *Dune Pioneers*

This community is present adjacent to the northern and southern beaches of the study area. The main plant is *Scaevola thunbergii,* which is essential in the dune build-up as sand collects around its branches. Other common plants are *Arctotheca populifolia* and *Gazania rigens* var. *uniflora.*

Since 1937 the area occupied by this community has increased, because new areas suitable for dune pioneers have formed at the Richards Bay New Mouth area and along the southern part of the coast. Consistent mapping of this community from air photos is difficult because it is sometimes masked by intense reflection from the beach sand. The poorer quality of the air photos of 1937 impairs comparison with the photos of 1976.

6. Passerina rigida *Low Scrub*

This community follows the dune pioneer community in the succession and is characterized by the presence of the shrub *Passerina rigida.* In 1976 it formed a 1,5 km long band of vegetation between the Dune Pioneers and the Closed Dune Scrub north of the Mlalazi Estuary Mouth. Since 1937 this vegetation band has been displaced seawards by about 30 m. The landward side of the band has been invaded by Closed Dune Scrub and seawards, this community has encroached onto the Dune Pioneer Community. This denotes the advance of succession and is similar to that reported from south of the Mlalazi Mouth (Moll, 1972; Weisser *et al.*, 1982) and other parts of Natal e.g. Isipingo (Ward, 1980). As primary succession proceeds, a slow seaward expansion of this community can be expected, whereas on the landward side an encroachment of Closed Dune Scrub into the *P. rigida* Scrub will occur.

A future expansion of this community will depend on the availability of areas of Dune Pioneer Community that can be invaded. If, as is expected, the sand supply for this coastal zone increases and a consequent increase of Coastal Dune Pioneer communities results, an increase in area of this scrub community will take place.

7. *Cultivation, old lands and Secondary Mixed Dune Grassland and Dwarf Shrubland*

This mapping unit covered the largest area in 1937. This was the result of destruction of the original forest by humans, through fire, clearing of forest for cultivation and grazing. The 1957 air photos show a reduced area of this mapping unit, whereas in 1976 only isolated, minor patches are present.

The mapping unit presents a varied picture, such as cultivated fields, old lands, grasslands dominated by grasses such as *Imperata cylindrica* to a dwarf shrubland with species such as *Chrysanthemoides monilifera* and *Helichrysum* spp. Secondary succession of the complex of communities included in this mapping unit will in time lead to Secondary *Acacia karroo* Woodland or a Secondary Dune Scrub and a Secondary Dune Forest (Fig. 5).

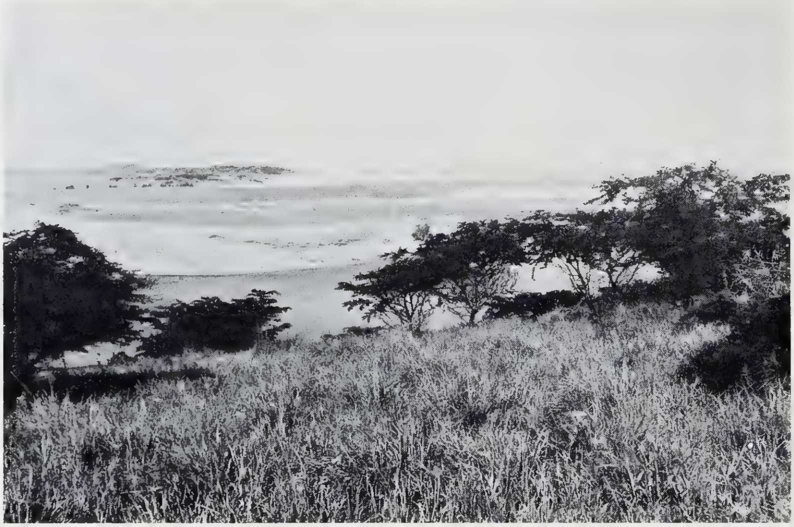

FIG. 3.—New mouth region (Map 1) of the Richards Bay Sanctuary, with sand areas colonized by dune pioneers (centre). The Secondary Dune Grassland shows an invasion by *Acacia karroo* that will form a woodland later.

After the control of this area was taken over by the Department of Forestry during 1952, most of the area classified in this mapping unit was afforested with *Pinus* and *Eucalyptus* and *Casuarina equisetifolia* was planted in rows as wind breaks (Fig. 5).

Areas not afforested are, in the absence of fire, grazing and ploughing, rapidly invaded by woody vegetation such an *Acacia karroo* Woodland (Fig. 3), including species such as *Allophyllus natalensis, Clerodendron glabrum, Rhus nebulosa* and *Apodytes dimidiata.*

If present management conditions persist, the secondary grasslands and dwarf shrublands will disappear and be replaced mainly by *Acacia karroo* Woodland, Secondary Scrub and Secondary Forest. This conclusion was also reached by Weisser (1978a) for the grasslands north of Richards Bay.

8. *Secondary* Acacia karroo *or* Trema orientalis *Woodland with occasional Secondary Scrub*

As found in other areas (e.g. Edwards, 1967; Weisser, 1980) *Acacia karroo* is a frequent invader of abandoned fields, Secondary grassland (Fig. 3) and dwarf shrubland communities. During field checking, it was discovered that some areas at Richards Bay interpreted as *Acacia karroo* Woodland were in fact *Trema orientalis* groves. Therefore, *Trema orientalis* stands were included in this mapping unit. MacDonald & Pammenter (MS.) reported *Trema orientalis* as the main woody species in the regeneration of a Coastal Dune Forest after fire. This suggests that the *Trema orientalis* areas found have been affected by fire.

Acacia karroo Woodland has occupied most of the habitat suitable for its development and only a slight increase of the *Acacia karroo* area is expected in the future. However, because *Acacia karroo* is a successional stage of development towards Secondary Dune Scrub and Forest, older parts will progressively be taken over and *Acacia karroo* Woodland will diminish under the present management (Fig. 5).

9. *Secondary Dune Scrub, Secondary Dune Forest and Degraded Dune Forest*

This is a complex mapping unit of primary and secondary forest areas, with limits that were difficult to map, especially in relation to the often adjacent Climax Dune Forest. This mapping unit is mainly found at the northern and southern end of the study area.

In the short term, under the present management, an increase of this unit can be expected, as old *Acacia karroo* Woodlands are replaced in the succession by Secondary Dune Forest. In the long term, a decrease will occur, when the Secondary Dune Forest evolves to Climax Dune Forest (Fig. 5).

10. *First Seaward Dune Slope, usually with Closed Dune Scrub and Low Forest*

This mapping unit forms an almost continuous band of woody vegetation along the coast and is exposed to seawinds on the usually steep seaward slope of the dunes. The canopy frequently shows windpruning owing to exposure to saltspray-bearing seawinds. The landward limit was established stereoscopically, taking the upper limit of the first seaward slope as the boundary. On eroding coastal stretches this mapping unit includes newly exposed substrates that tend to be colonized by pioneers (Fig. 2) and about 25 'arcuate scars' (*vide* Weisser, 1978b). These arcuate discontinuities in the dune barrier are caused by erosion when a water spring is present.

Since 1937, the area of this mapping unit increased at the expense of drift sands and decreased because of erosive processes in the central part of the study area. Dune slumping causes the destruction of Closed Dune Forest and, more rarely, of Climax Dune Forest (Fig. 2).

Where primary and seral stages of secondary vegetation are present today, a progression towards the climax is expected. Some areas may be affected by coastal erosion in the future.

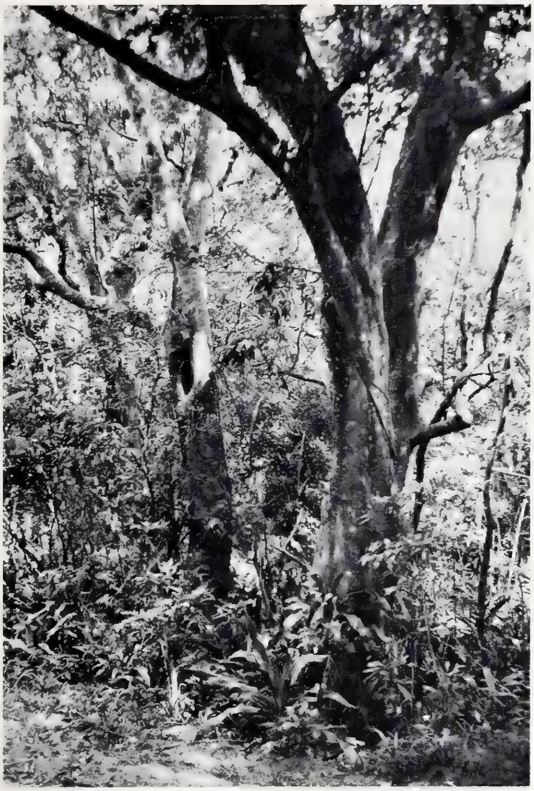

FIG. 4.—Dune Climax Forest on the road to the Richards Bay Sanctuary Mouth with tall *Celtis africana* trees and *Dracaena hookeriana* in the undergrowth.

11. *Climax Dune Forest*

The Climax Dune Forest (Fig. 4) consists of a few tall dominant trees with a poorly developed understorey and often dense fieldlayer with *Isoglossa woodii.* Additional information on this type of vegetation can be obtained from Venter (1972) and Weisser (1978 & 1980).

Climax Dune Forest probably covered most of the study area before colonization by man. Relations with other mapping units are shown in Fig. 5. By 1976, owing to clearing for shifting cultivation and grazing, it had dwindled to an area of about 20 ha on the Mlalazi Peninsula, some minor isolated pockets mainly near the coast and some forest areas near Richards Bay.

The delimitation of this mapping unit from Secondary Dune Scrub and Secondary Forest is often difficult because they are similar on the air photos. Therefore the limits obtained must be regarded as tentative. The diminishing trend of this primary Dune Forest was stopped by conservative management of the Forestry Department as from 1952.

From the conservation point of view, this mapping unit is most important, as it represents what was typical for the dune before the advent of man in the area (Weisser, 1978b). If the present management for protection against human interference and fire continues, the area of climax forest will not be diminished.

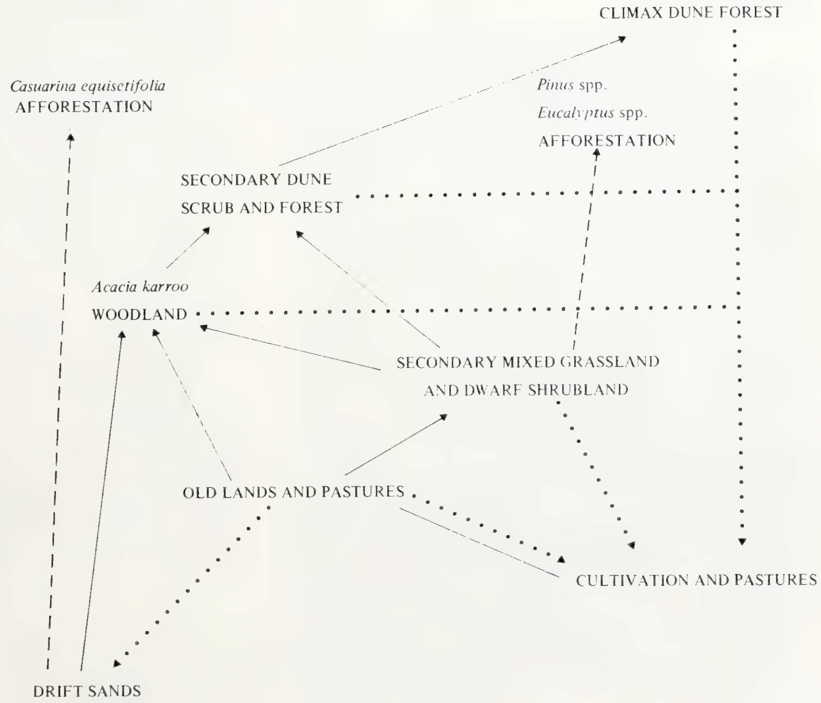

FIG. 5.—Successions (solid lines), retrogressions (stippled lines), and afforestation (dashed lines) pathways as shown on aerial photos from 1937 to 1976 after clearing of Climax Dune Forest.

12. Casuarina equisetifolia *Afforestation*

Casuarina equisetifolia was extensively and successfully used to stabilize drift sands by planting it in rows as wind breaks. This mapping unit is mainly found on drift sands (Fig. 5).

Most areas suitable for this species have been planted and little or no increase in area is expected.

13. Eucalyptus *and* Pinus *Afforestation*

Most of the Secondary Mixed Grassland and Dwarf Shrubland of 1937 are today covered with *Pinus* and *Eucalyptus* forests (Fig. 5). The main plantations are located in the central portion of the study area.

A few areas suitable for afforestation are still available, and they will probably be used in the near future. However, if plans for a Botanical Garden for Kwazulu (K. Cooper, pers. comm.) are implemented, some areas will, after harvesting, be allowed to revert to communities with indigenous species.

14. *Kraal areas*

On the 1937 air photos 77 kraal areas were detected. With the take-over by the Forestry Department, the people moved and no kraals were found on the air photos of 1976.

15. *Areas occupied by Forestry facilities*

These areas include human dwellings, firetowers and their surroundings belonging to the Department of Forestry and are of limited extent.

Vegetation maps

Six vegetation maps for 1937 and six for 1976 at a scale of 1: 10 000 were completed and are available for inspection and use at the Botanical Research Institute.

DISCUSSION AND CONCLUSIONS

The presence of continuous dune forest in undisturbed dune areas south and north of the study area, at, for example Mtunzini and Mapelana, and the relics of Climax Dune Forest in the study area itself on the Mlalazi Peninsula and near Richards Bay support the hypothesis that Climax Dune Forest covered most of the dune barrier before the colonization of man. Iron age human settlement of the Zululand Coast probably dates back to the fourth century A.D. (Hall & Vogel, 1978).

Keet (1936) reports the formation of drift sands owing to (1) cultivation on dunes; (2) trampling of vegetation by stock; (3) paths and roads; (4) veld-burnings; and (5) excessive clearing of scrub. Air photos of the study area bear out these observations. Many kraals, recent and old fields and paths found in the dune area provide evidence of occupation. The validity of these observations for the Zululand Coast is confirmed by Stephens (1939), who visited the Zululand Dunes in 1938 and described the human settlement and its effect on the vegetation.

Fig. 5 schematically represents the knowledge on vegetation dynamics after Climax Dune Forest destruction as shown on air photos. The great differences on the vegetation maps of 1937 and 1976 are the consequence of human occupation of the dunes. They are related to the needs of people for space, habitation, fuel wood, grazing lands and croplands. Because of the loss of fertility of the dune soils after a few years of cultivation, the inhabitants shifted and cleared new dune forest areas. In this way a large area was affected by a small population.

Abandonment of fields induced secondary, post cultivation plant successions. Many old lands were found covered with *Acacia karroo* Woodland, a Secondary Dune Scrub or Secondary Dune Forest.

These results are similar to those reported for the dune area at the Richards Bay-Mfolozi Mouth by Weisser & Marques (1979) and confirm the high degree of vegetation degradation caused in the past by shifting cultivation, fire and grazing on the Zululand Coast. The rapid vegetation recovery through secondary plant successions, once protective measures by the Department of Forestry were enforced, was also confirmed.

The future of the vegetation will depend on the management applied to the area. If the Forestry Department of Kwazulu continues the management system applied since 1952, the plantation areas will continue to be used for afforestation and some Secondary Grassland and Secondary Shrubland areas will be additionally afforested. *Acacia karroo* Woodland will invade some of the grasslands and dwarf shrublands and, in time, develop into Secondary Dune Forest. Present-day *Acacia karroo* and *Trema orientalis* Woodlands will develop into Secondary Dune Forest. Secondary Dune Forest present today will mature becoming more like the original Dune Forest (Fig. 5).

Extensive vegetation changes since 1937 were found documented on air photos, an estimated 80% of the mapping units having changed since 1937. At the time, most of the Climax Dune Forest had been destroyed and replaced by fields and post cultivation seral stages, mainly Secondary Dune Grassland and Dwarf Shrubland, *Acacia karroo* Woodland, Secondary Dune Scrub and Secondary Dune Forest. In three places where the vegetation cover was completely destroyed, inland drift sands originated.

During the 1950's, the Forestry Department caused a shift in vegetation trends by removing the inhabitants from the dunes, enforcing protection against fire, grazing and further clearing, and implemented an afforestation programme.

The 1976 air photos show forest plantations as a main feature of the study area and secondary, unafforested areas with more dense vegetation cover. Under the management of the Department of Forestry, the recovery of secondary vegetation has been rapid, usually leading through an *Acacia karroo* Woodland of Secondary Dune Scrub to a Secondary Dune Forest.

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Floristic and structural features of the coastal foreland vegetation south of the Berg River, western Cape Province, South Africa

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ABSTRACT

Floristic and structural features of the three main vegetation types found in the coastal foreland of the western Cape Province, south of the Berg River, are outlined. Coastal Renosterveld, which occupies 6% of its former extent, is the most threatened type, followed by Coastal Fynbos (14%) and West Coast Strandveld (41%). Coastal Renosterveld is closely related to Mountain Fynbos vegetation found on clay-rich soils together with West Coast Strandveld inclusions in specific habitats. Coastal Renosterveld is the product of recent regular disturbance by a short interval burning regime and overgrazing.

RÉSUMÉ

TRAITS FLORISTIQUES ET STRUCTURAUX DE LA VÉGÉTATION DE L'AVANT-PAYS CÔTIER DE LA RIVIÈRE BERG, DANS LA PROVINCE OCCIDENTALE DU CAP EN AFRIQUE DU SUD

Les traits floristiques et structuraux de trois types de végétation trouvés dans l'avant-pays côtier de la Province occidentale du Cap, au sud de la rivière Berg, sont esquissés. Le Renosterveld Côtier, qui occupe 6% de son étendue antérieure, est le type le plus menacé, suivi par le Fynbos Côtier (14%) et le Strandveld de la Côte Occidentale (41%) Le Renosterveld Côtier est étroitement apparenté à la végétation du Fynbos de Montagne trouvée sur des sols riches en argile avec des enclaves de Strandveld de la Côte Occidentale dans des habitats spécifiques. Le Renosterveld Côtier résulte d'une perturbation régulière récente consistant en un régime de brûlage à courts intervalles et un surpâturage.

INTRODUCTION

The Cape Floral Kingdom (Good, 1974; Takhtajan, 1969) is concentrated in the region known as Capensis (Taylor, 1978; Walter, 1973). The western part has a distinctly mediterranean-type climate with dry summers and wet winters, but eastward the rainfall becomes increasingly non-seasonal (Taylor, 1980). The region is bounded to the north and east principally by the Karoo-Namib Region together with some outliers of the Sudano-Zambezian and Afromontane Regions (Taylor, 1980; Werger, 1978; Werger & Coetzee, 1978; White, 1978).

The Capensis vegetation has recently been subdivided into two main formations, namely, the heathlands on oligotrophic soils which are called fynbos (Kruger, 1979) and mediterranean-type shrublands, the scrub formations found on the more fertile soils, called renosterveld and strandveld (Boucher & Moll, 1981; Di Castri, 1981).

The indigenous vegetation of the coastal foreland of the western Cape Province, between the Berg River and False Bay is described in this paper. Structural and floristic features of the vegetation are related to variations in the habitat. Some tentative suggestions on the affinities between the local veld types (Acocks, 1975) and their derivation are presented. The main vegetation types shown in Fig. 1 are based on the interpretation of 1: 10 000 scale orthophoto maps, on data obtained from the intensive study of three east-west transects through the area, and on field experience. Island outliers of Mountain Fynbos, which occur on upland sites, are not described in this article.

A variety of geological substrates of various ages is exposed in the western coastal foreland which contribute to the ecological diversity of the vegetation. The oldest substrates are the Late Precambrian Malmesbury Group shales which are intruded by Cape granites and are overlain by Klipheuwel and Table Mountain Group sandstones and shales with Mesozoic to Cainozoic limestones, calcretes and sands on top.

The western Cape has been inhabited by hunter-gatherers since the Late Pleistocene and by herders for at least the last 2000 years (Avery, 1975). Nomadic Khoisan or Hottentot tribes used fire to stimulate vegetation regrowth for grazing purposes, a habit adopted by European man subsequent to his arrival here in 1652. Fires caused by lightning and by rock falls are considered to be a natural phenomenon in the mountains of the south-western Cape (Taylor, 1978) and they would presumably have spread from there to the adjacent lowland areas.

European man has destroyed large areas of the coastal foreland vegetation through his unrelenting quest for grazing, for fuel and for arable land. This vegetation has been depleted to the extent that at most only 14,7% of the western coastal foreland vegetation remains in a reasonably natural state today. Table 1 outlines the degree to which the three veld types in this area, namely, West Coast Strandveld, Coastal Renosterveld and Coastal Fynbos, have been reduced through the activities of man. Coastal Renosterveld is by far the most threatened of these veld types.

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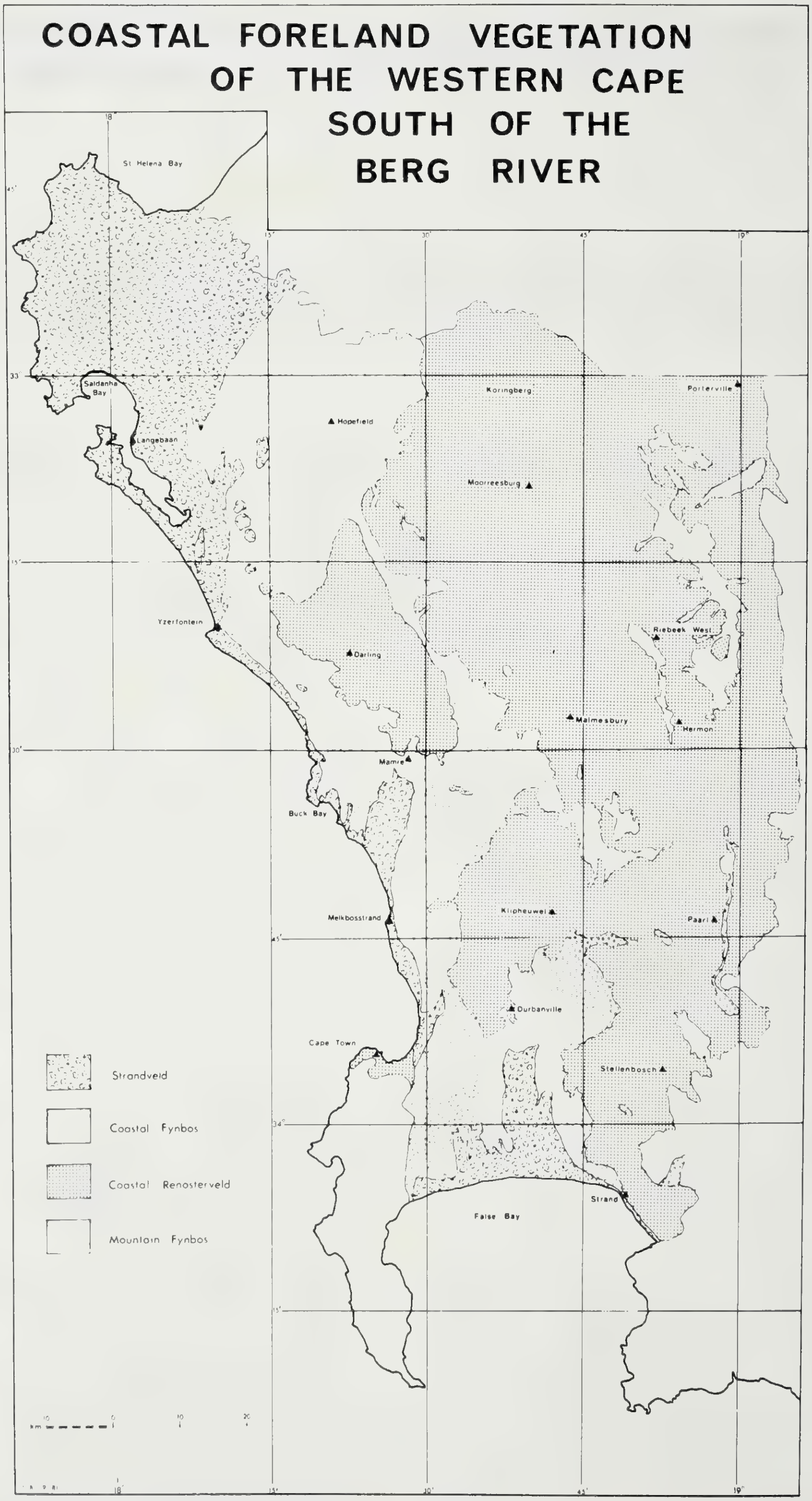

FIG. 1.—Coastal foreland vegetation of the western Cape south of the Berg River.

TABLE 1.—Remaining natural vegetation in the western Cape foreland south of the Berg River in 1972. Extracted from the 1972 series of 1:10 000 scale orthophoto maps

Veld Type	Original area (ha)	Remaining area (ha)	Percentage left
West Coast Strandveld	177 266	74 195	41%
Coastal Fynbos	295 860	41 239	14%
Coastal Renosterveld	512 266	29 502	6%

WEST COAST STRANDVELD

Strandveld vegetation is found on calcareous dune sands, calcretes, limestones, weathered granites and shales.

Mature, West Coast Strandveld communities are dominated by a fairly continuous canopy of sclerophyllous, nanophyllous to microphyllous, divaricately branched, nanophanerophytes such as *Chrysanthemoides incana, Colpoon compressum, Euclea racemosa, Olea exasperata* and *Pterocelastrus tricuspidata* forming a 1,0–2,5 m tall scrub. The West Coast Strandveld is commonly referred to as a broad-leaved sclerophyllous scrub. Deciduous, succulent-leaved nanophanerophytes such as *Othonna floribunda* and *Zygophyllum morgsana* are usually present (Boucher & Jarman, 1977). Chamaephytes generally form a lower shrub layer with perennial grasses abundantly interspersed up to 1,0 m tall. Typical species of the lower shrub layer are *Ehrharta calycina, E. villosa, Limonium perigrinum, Ruschia caroli, Tetragonia fruticosa* and *T. spicata.* A high proportion of the West Coast Strandveld shrubs, dwarf shrubs and even annuals have succulent leaves or stems. Deciduous-leaved geophytes are regularly encountered and the annual flora often provides mass displays of colour in spring particularly in disturbed areas (Acocks, 1975; Boucher & Jarman, 1977; Boucher & Moll, 1981; Taylor, 1978).

Strandveld vegetation is very variable, for instance the sandy littoral generally supports prostrate, spreading succulent chamaephytes, while small patches of a tall broad-leaved sclerophyllous scrub, up to about 3,5 m high, with a closed canopy can develop in isolated sheltered positions between the dunes. The dominant species in these latter situations are *Euclea racemosa* and *Sideroxylon inerme.*

Scattered clumps of *Willdenowia striata* and emergent *Thamnochortus* spp. (Restionaceae), associated with a depauperate West Coast Strandveld vegetation, occur with increasing abundance as the distance from the sea increases, together with marginal fynbos species belonging to the Fabaceae (*Aspalathus*), Polygalaceae (*Muraltia* and *Nylandtia*), Rutaceae (*Agathosma* and *Diosma*) and Thymelaeaceae (*Passerina*). Ericaceae and Proteaceae are not found in West Coast Strandveld vegetation.

COASTAL RENOSTERVELD

This veld type is found on shales and granites in a rainfall zone of 250–550 mm per annum. Typically, Coastal Renosterveld consists of a matrix of cupressoid and leptophyllous, orthophyllous, divaricately branched shrubs, particularly Asteraceae such as *Athanasia trifurcata, Elytropappus rhinocerotis, Eriocephalus africanus, Felicia filifolia, Metalasia muricata* and *Stoebe spiralis* 1–2 m tall. *Anthospermum aethiopicum* (Rubiaceae) is generally abundant and geophytes belonging to the families Iridaceae, Liliaceae and Oxalidaceae are important components of the basic Coastal Renosterveld matrix. Perennial grasses such as *Cymbopogon marginatus, Pentaschistis* spp. and *Themeda triandra* become locally abundant with annual European grasses and herbs common in very disturbed situations. Restionaceae are seldom dominant, but can usually be found in this veld type. Randomly scattered bush clumps through the Coastal Renosterveld matrix are dominated by the sclerophyllous evergreen tree, *Olea europaea* subsp. *africana*. The margins and interior of these 2–4 m tall *Olea* patches are commonly dominated by deciduous, orthophyllous, microphyllous, nanophanerophytes, particularly a number of *Rhus* species. Hemicryptophytes and geophytes are usually abundant in the herbaceous stratum. These bush clumps are associated with *Microhodotermes viator* termitaria which have been present in the area for the last one million years (J. J. N. Lambrechts, pers. comm.). These bush clumps are also usually clustered around rock outcrops and drainage lines, probably because of more favourable, moist, local conditions.

For at least a decade or two these old lands retain an overwhelming dominance of the Asteraceae found in the general Coastal Renosterveld matrix. Single robust *Elytropappus rhinocerotis* individuals have been found to persist for at least 50 years.

Coastal Renosterveld is not generally considered to be a true Cape heathland vegetation because it lacks the constant presence of the ericoid component (Taylor, 1978), although Ericaceae are not entirely absent from this veld type.

COASTAL FYNBOS

This heathland vegetation occurs on leached acid sands which accumulate from the *in situ* weathering of granites and sandstones, or as wind blown accumulations of sand from rivers or estuaries, or on leached maritime dunes. The sands vary in depth from less than a metre to more than 70 m.

The typical form of this veld type is dominated by ericoid, narrow leptophyllous, evergreen, divaricately branched shrubs and rhizomatous hemicryptophyters 0,75–1,50 m tall. Taller, up to 2,5 m high, micro- to mesophyllous, sclerophyllous, shrubs increase towards the margins of the Coastal Fynbos where the sand is shallower. Annual herbs and geophytes occur throughout, but they do not assume the same proportions found in either the Coastal Renosterveld or the West Coast Strandveld. The low nutrient status of the substrate is probably responsible for the virtual absence of the invasive European annual flora. In contrast, this treeless vegetation (Campbell *et al.*, 1979; Kruger, 1979; Levyns, 1961) is very susceptible to invasion by trees and tall shrubs from the Australian heathlands, such as *Acacia* spp. and *Eucalyptus* spp. *Leptospermum* spp., and by *Pinus* spp. from the northern hemisphere heathlands.

The Coastal Fynbos is a complete fynbos vegetation dominated by typical Cape elements, namely, Proteaceae, Restionaceae and by ericoid-leaved shrubs, although not by Ericaceae. Three of the five endemic Cape families, Bruniaceae, Penaeaceae and Stilbaceae are found. It is characterized by the presence of *Erica mammosa, Phylica cephalantha, P. stipularis, Thamnochortus obtusus* and *T. punctatus.* Acocks (1975) referred to 'an easy transition' between Coastal Fynbos and its adjacent Coastal Renosterveld and West Coast Strandveld vegetation in which large clumps of *Willdenowia striata* (Restionaceae) become particularly evident. These veld types are, however, quite distinct, although local patches of West Coast Strandveld, associated with calcrete outcrops, and of Coastal Renosterveld, associated with partially exposed termitaria or granite outcrops, occur within Coastal Fynbos.

DISCUSSION

The West Coast Strandveld in the arid winter rainfall area of Namaqualand has a more open canopy than in the western Cape and the vegetation is generally shorter. Succulents become more prominent and the vegetation assumes the appearance of Succulent Karoo after disturbance. Scrub forest patches are far more common in the strandveld east of False Bay, where the summer drought is less severe (Boucher & Moll, 1981; Taylor, 1961, 1978; Von Breitenbach, 1974). The West Coast Strandveld plants react to the dry summer and wet winter periods in an expected fashion, growing when it is wet and being generally dormant in the dry period. The dominant broad-leaved sclerophyllous scrub species all sprout after fires. The West Coast Strandveld is, therefore, a typical mediterranean-type climate shrubland vegetation of lime-rich sandy soils adapted to a fire regime.

Some component species of the western Coastal Fynbos are apparently out of phase with their environment in that they grow during the dry summer period. A high proportion of the Coastal Fynbos species have very small or reduced leaves, a low proportion of succulence and the perennial herbaceous flora is largely hard and stiff with reduced leaves and photosynthetic stems. These conditions are possibly an adaptation to the low nutrient status of the substrate where it is advantageous to utilize the meagre nutrient resources efficiently, as soon as they become available, without wasting them in the production of unnecessary vegetative parts. They also have anatomical adaptations to use water economically (Cutler 1972; Low, 1980; Specht, 1979; Specht *et al.*, 1980).

The ability of western Coastal Fynbos to survive under low rainfall minima is indicated by its presence in the semidesert conditions of Namaqualand in a rainfall of around 100 mm *per annum*. This contrasts markedly to the Coastal Fynbos in the Knysna area of the southern Cape, which receives a mean annual rainfall of about 1 400 mm per annum and occurs alongside tall temperate forests. The low rainfall (100–700 mm *per annum*), the summer soil moisture deficits and the periodic fires have been suggested as reasons for the absence of indigenous trees in the western Coastal Fynbos (Campbell *et al.*, 1979).

Coastal Fynbos is far more uniform in composition than Mountain Fynbos, possibly because of the uniformity of the sandy plains in contrast to the great variety of niches present in the folded mountains of the Cape.

Coastal Renosterveld is akin to the Californian Coastal Sage (Rutherford, 1978; Taylor, 1978) in that it is the product of a disturbed environment. This condition is shown by the overwhelming dominance over large areas by a few species with pioneering abilities. It is tempting to postulate about the development of the Coastal Renosterveld to its present state. Species which can become dominant in pelitic upland fynbos, that is Mountain Fynbos on weathered granites or shales, are either dominant or are scattered through the Coastal Renosterveld. These species that are mainly confined to the shrubby matrix of the Coastal Renosterveld are largely unpalatable seed regenerating species with a short maturation period of maximally five years (e.g. the dominant Asteraceae), or sprouting species of Ericaceae (*Erica sparsa*), Proteaceae (*Leucadendron salignum*) and Restionaceae (*Restio cuspidata*), or geophytes (*Watsonia* spp.). Fifty-four percent of the species found in a recent survey to be restricted to the Coastal Renosterveld have also been recorded in the Mountain Fynbos vegetation of the Jonkershoek State Forest. The remaining bush clump species on termitaria and around granite rock outcrops in the Coastal Renosterveld are largely sprouting species, geophytes and annuals which are structurally and floristically allied to the West Coast Strandveld.

The overwhelming contribution of species which can withstand recurrent five yearly fires is indicated in Table 2 for the western coastal lowland.

The conclusion drawn is that the western coastal foreland vegetation is the product of disturbance that probably took the form of repeated short interval fires, overgrazing and the collection of firewood (Acocks, 1979; Killick, 1979; Kruger, 1979; Levyns, 1929, 1950, 1956; Story, 1952).

Present day longer intervals of more than ten years between fires and the almost complete

TABLE 2.—Mode of regeneration of perennial species restricted to each of the three veld types in the coastal foreland of the western Cape (data based on observation and the analysis of sample data)

Veld Type	Number of samples	Number of species	Geo-phytes	Hemicrypto-phytes	Sprouting shrubs	Succu-lents	Seeders maturing in < 5 yrs	Seeders maturing in > 5 yrs
West Coast Strandveld	105	84	15%	10%	29%	25%	21%	—
Coastal Renosterveld	133	181	22%	13%	27%	7%	30%	1%
Coastal Fynbos	54	66	5%	18%	45%	3%	26%	3%

destruction of the larger indigenous fauna, including both predators and grazers, has allowed a continuous shrub canopy to develop in undisturbed areas of Coastal Renosterveld. The herbaceous flora has consequently become depleted under these conditions through shading and through increased termite activity.

The extensive cultivation of annual wheat crops, together with the continued general destruction of the indigenous vegetation, particularly through overgrazing, has led to soil erosion and a generally drier soil climate in which the West Coast Strandveld flora, particularly the succulent component, is becoming more conspicuous in areas now supporting Coastal Renosterveld.

CONCLUSIONS

The West Coast Strandveld, Coastal Fynbos and Coastal Renosterveld all appear to be types that have been exposed to a relatively short interval fire regime and to heavy grazing. This is a relatively recent phenomenon, probably related to the appearance about 2 000 years ago of pastoral Khoisan (Hottentot) tribes, who used fire to improve the grazing for their flocks of sheep and cattle. Subsequent to their settlement here 300 years ago, European settlers adopted this practice in an uncontrolled fashion, despite repeated legislation and heavy fines designed to curb this habit (Botha, 1924). It might reasonably be postulated that the present composition and structure of the lowland vegetation, particularly of the treeless Coastal Fynbos, is due to the very recent introduction of a short interval fire regime under which a tree flora must still evolve. The success of the acacias, pines and eucalypts in the Coastal Fynbos suggests, however, that the evolution of an indigenous tree flora might never take place because this so-called 'vacant niche' will have been occupied.

Unvegetated expanses of sand accompany overgrazing in Coastal Fynbos and result in longer intervals between fires. The systematic burning of this veld type to obtain better grazing has been superseded recently, in parts by brush-cutting. This system benefits the sprouting plants, particularly the Restionaceae, which achieve an overwhelming dominance to the detriment of seed regenerating species. This degradation is equivalent to that of Coastal Renosterveld and West Coast Strandveld, under a short interval burning regime coupled with overgrazing where the stages of degradation go from dominance by scrub, to shrubs, to low inedible dwarf shrubs, particularly succulents, to perennial herbs and finally to dominance by annuals. This degradation is considered to be related to a general drier soil climate.

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Savannas of southern Africa: attributes and use of some types along the Tropic of Capricorn

F. VAN DER MEULEN* and H. A. M. J. VAN GILS**

ABSTRACT

Two recent reconnaissance vegetation surveys of savanna in the Kalahari of Botswana and in the western Transvaal (RSA) carried out on a landscape basis are described. Attributes and utilization of four selected stations along a transect of about 1 000 km near the Tropic of Capricorn, with a climate changing eastward from arid to subhumid, are compared. The stations represent microphyllous *Acacia*-savannas and mesophyllous *Burkea–Ochna–Terminalia* savannas on deep red sands, covering extensive parts in both survey areas. Land attributes used are physiography, macro-climate, vegetation (growth), large herbivores and land use practices.

The most striking difference between the four areas are the land use practices.

Some notes on the survey methodology are presented. The authors conclude that for small-scale vegetation-land use surveys the 'holistic' landscape approach can be recommended.

RÉSUMÉ

SAVANES DE L'AFRIQUE DE SUD: CARACTÉRISTIQUES ET EXPLOITATION DE CERTAINS TYPES LE LONG DU TROPIQUE DU CAPRICORNE

Deu prospections récentes de la végétation de savane dans la zone du Kalahari au Botswana et dans le Transvaal occidental, basies sur sa physionomie, sont décrites. Les caractéristiques et l'exploitation de quatre sites choisis le long d'un transect d'environ 1 000 km près du Tropique du Capricorne, avec un climat passant de l'aride en ouest au sub-humide à l'est, sont comparées. Les sites représentent des savanes à Acacia *microphylles et des savanes à* Burkea–Ochna–Terminalia *mésophylles sur sable rouge profond couvrant de vastes superficies dans les deux zones prospectées. Les caractéristique du terrain utilisées sont la physiographie, le macroclimat, la végétation (croissance), les grands herbivores et l'utilisation des sols.*

La différence la plus marquante entre les quatre sites réside dans l'utilisation des sols.

Quelques notes sur la méthodologie de la prospection sont présentées. Les auteurs concluent que pour des prospections à petite échelle de la végétation et de l'utilisation des sols, l'étude 'holistique' du paysage peut être recommandée.

INTRODUCTION

Recently, some reconnaissance vegetation-land (use) surveys have been carried out in savannas of the Sudano-Zambesian Region in southern Africa. Extensive areas were mapped in the Republic of Botswana and the Transvaal Province, Republic of South Africa. The Botswana survey (CARAP, 1980) contains an inventory of the range and game resources of the Kalahari in southern and western Botswana, approximately 240 000 km^2 in size, with final mapping scale at 1: 1 500 000, including more detailed maps at scales of 1: 150 000 and 1: 50 000 of a selected area. The Transvaal study (Van der Meulen, 1979) covers about 25 000 km^2 in the western Transvaal and concentrates on taxonomy and ecology of the plant communities. Final mapping was done at scale 1: 250 000 (Van der Meulen & Westfall, 1979).

Intensive use was made of black and white air photos (scales 1: 20 000–1: 70 000) and LANDSAT-imagery with stratified field sampling more or less according to the Braun-Blanquet method. Because of the small mapping scales, final maps show whole land units which are based not only on their vegetational features, but also on other land attributes like macro-climate, landform, soil and sometimes even the main land use practices.

The survey areas together roughly present a broad strip of land extending about 1000 km from west to east near the Tropic of Capricorn (Fig. 1). Along this transect from the Kalahari Basin of Botswana eastward onto plateau areas of Transvaal, the climate changes from arid to subhumid. Results of the two surveys enable us to compare attributes and utilization of some savanna types along this climatic gradient. The comparison supports our view that small scale vegetation surveys should be carried out on a landscape basis, that is, to include land attributes other than vegetation alone in the survey and the mapping procedure.

ENVIRONMENT

A brief general description is given of the physical environment of the transect area, dealing with main changes in climate from southern Botswana eastward into Transvaal.

Southern Africa is part of the great African plateau, one of the greatest plateaux of the earth's surface, stretching from the Cape Province to the southern limits of the Sahara. Geographically, southern Africa consists of a fairly flat high interior plateau, fringed on either side by strips of coastal

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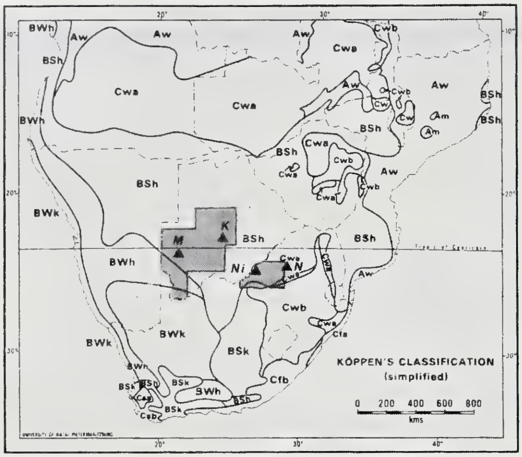

FIG. 1.—Reconnaissance vegetation survey areas (dark) and four selected stations (▲) near the Tropic of Capricorn, plotted on Köppen's classification of climates for southern Africa (Schulze & McGee, 1978). M=Matsheng; K=Kuhtse; Ni=Nietverdiend; N=Nylsvley.

plains along the Pacific Oceans (Wellington, 1955). Our transect area lies on this plateau at about 24° southern latitude. It extends between 21°–28° eastern longitude (Fig. 1). Unlike the coastal strips, the plateau has a strong continental type of climate, designated in the Köppen system as Bsh. This is a dry and hot steppe climate of arid zones with summer rainfall. Mean annual temperature is over 18°C.

Within the Bsh climate type, differences occur along the transect, the climate being warm and dry in southern Botswana, becoming cooler and moister eastward into Transvaal (Schulze & McGee 1978, see also Table 1; Fig. 2). Mean annual precipitation ranges from 200–400 mm in the west to 600–800 mm in the east, whereas the percentage of seasonal variability from mean annual rainfall is much higher in the west (up to about 70%). Throughout the transect area, the rain season is about 5–7 months long. Rain falls in summer. Temperature differences are only pronounced in this season: January average daily maximum temperatures range between 35°/32°C–30°/27°C from west to east and average daily temperatures range between 26°/28°C–22°/20°C. Evaporation varies between 600/800 mm–200/400 mm per year in the same direction (Table 1).

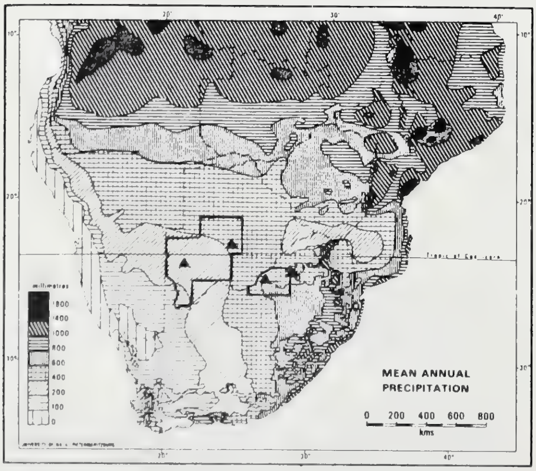

FIG. 2.—Mean annual precipitation for southern Africa. From Schulze & McGee (1978). Survey areas demarcated. Compare with Fig. 1.

General topography consists of gently undulating plains at an elevation of 1 100 m with low depressions and dunes in Botswana. In the western Transvaal, flats with plains at an elevation of about 1 100 m are surrounded by low hills up to 300 m. Soils are reddish arenosols, locally with halomorphic properties. Clays and lithosols are common in the Transvaal hills (Harmse, 1978). The difference in surface drainage is very conspicuous: rivers and wadi's are common in Transvaal. However, surface water in Botswana is rare.

VEGETATION-LAND SURVEYS: A COMPARISON OF RESULTS FROM BOTSWANA AND TRANSVAAL

To discuss the surveys in Botswana and Transvaal in detail is beyond our present scope. We refer to the respective reports. Our purpose is to compare some results from both surveys. In order to compare appropriate land characteristics we concentrate on sandveld tree-savanna types of slightly acid to neutral fersiallitic red sands. Such types cover extensive parts in both survey areas. They are composed either of microphyllous thorn trees (*Acacia* spp.) or of mesophyllous trees (*Burkea africana, Terminalia sericea, Ochna pulchra*). Four stations are selected along the transect, two in Botswana and two in Transvaal. From east to west these are: Matsheng, Kuhtse, Nietverdiend and Nylsvley (Fig. 1, Table 1). For each station data are supplied on the following land features:

(i) climate: type, precipitation, rain season, evaporation, temperature,
(ii) physiography: elevation, relief, soil type, soil pH, surface drainage,
(iii) vegetation: structure, dominant woody plants, dominant grasses, life form composition, phytomass (above ground standing crop), crude protein (CP), phosphorus (P), carrying capacity,
(iv) large herbivores: domestic livestock and wildlife species,
(v) land use types.

Matsheng village area provides an example of the *Acacia*-savannas which occur in the southern parts of the Botswana survey, and Kuhtse gives an example of the mesophyllous savannas in the northern parts. Similarly, Nietverdiend presents the microphyllous *Acacia*-savannas in the western Transvaal survey and Nylsvley* mesophyllous savannas. Both types in Botswana occur on plains and broad interdunal

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* This type was chosen because plant production data were available.

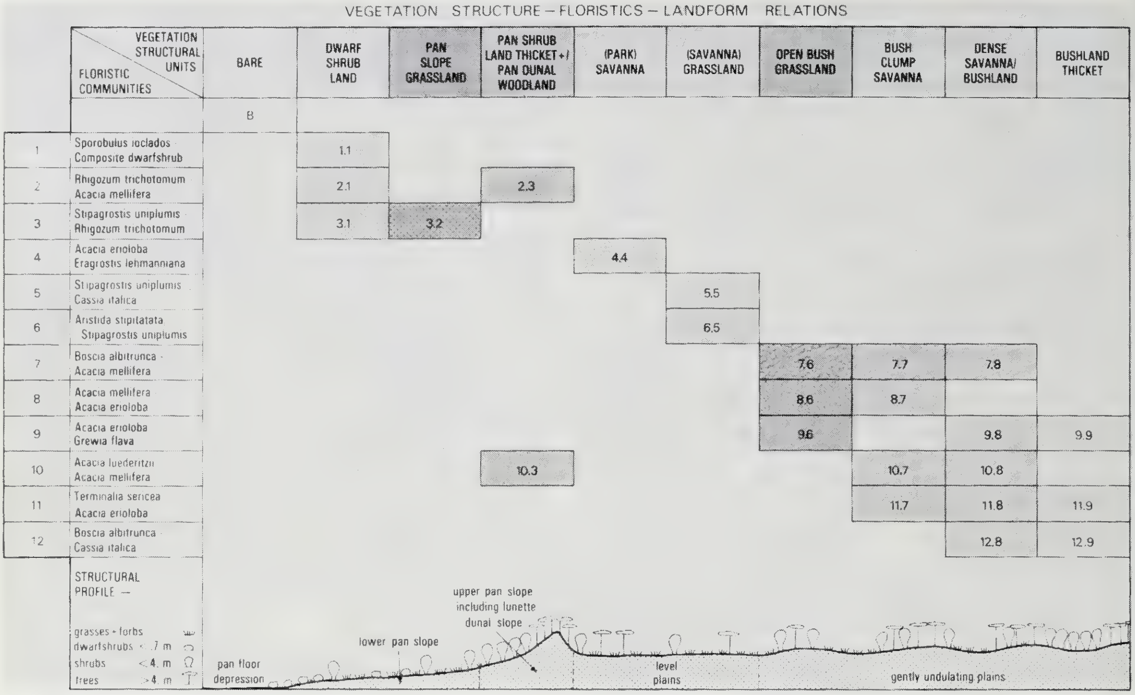
TABLE 1.—Land characteristics of savannas at four selected stations along a 1 000 km transect near the Tropic of Capricorn

STATION COORDINATES (S.lat.:E.long.)	MATSHENG 24.00 21.45	KUHTSE 23.15 24.30	NIETVERDIEND 25.00 26.00	NYLSVLEY 24.40 28.40
Climate				
type (Köppen system)	Bshw	Bshw	Bshw	Bshw
precipitation (mm/yr)	300	400	550–600	600–700
rain season	summer: 4–8 mnths	summer: 4–8 mnths	summer: 5–7 mnths	summer: 5–7 mnths
evaporation (mm/yr)	600–800	400–600	200–400	200–400
air temp (°C)				
average daily max. Jan.	32.5	31	27–30	27–30
average daily min. July	2.5	2.5	0–2.5	0–2.5
Physiography				*
region (Wellington, 1955)	Kalahari Basin Southern Kalahari	Kalahari Basin central Plain	Transvaal Plateau basin floor	Transvaal Plateau cuesta veld
elevation (m above sea level)	1 150	1 000	1 000–1 200	1 200–1 500
relief	(almost) flat	(almost) flat	(almost) flat; locally inselberge	undulating-gentle-moderately steep
soil type	fersiallitic sands	fersiallitic sands	fersiallitic sands	fersiallitic sands
soil pH	4–6	4–6	4–6	4–6
drainage (surface)	none	none	rivers; wadi's	rivers; wadi's
Vegetation				
physiognomy	microphyllous thorn savanna	mesophyllous broad-leaf savanna	microphyllous thorn savanna	mesophyllous broad-leaf savanna
predominant trees/shrubs	*Acacia erioloba* *A. luederitzii* *A. mellifera* *Boscia albitrunca* *Rhus tenuinervis*	*Terminalia sericea* *Ochna pulchra* *Burkea africana* *Lonchocarpus nelsii* *Bauhinia petersiana*	*Acacia erioloba* *A. fleckii- A. tortilis* *A. mellifera* *Boscia albitrunca* *Grewia flava*	*Terminalia sericea* *Ochna pulchra* *Burkea africana* *Combretum* spp. *Grewia flavescens*
predominant grasses	*Stipagrostis uniplumis* *Schmidtia* spp. *Eragrostis lehmanniana*	*Digitaria* spp. *Eragrostis pallens* *Antephora pubescens* *Eragrostis lehmanniana*	*Aristida congesta* *Schmidtia pappophoroides* *Eragrostis lehmanniana*	*Digitaria* spp. *Eragrostis pallens*
life form (cover %)				
macro-phanerophyte (> 8 m)	–	–	locally 1	1, locally 1–5
micro-phanerophyte (5–8 m)	2, locally ≤ 20	2, locally ≤ 20	1–5, locally 5–10	1–5, locally 5–20
nano-phanerophyte (< 5 m) multi-stemmed phan. (< 5 m)	2–20, locally 20	20, locally 2–20	1–10, locally 10–20	1–10, locally ≤ 25
woody chamaephyte	1	1	1	1
other chamaephyte	1	1	1	1
hemicryptophyte	30	40	30–35	30–60
therophyte	1	1	1	1
geophyte	1	1	1	1
phytomass (above-ground standing crop.: gr/m2 grasses + forbs)	50–160	70–160	?	90–180
C.P.	deficient	deficient	?	deficient
P.	deficient	deficient	?	deficient
carrying capacity (ha L.S.U.$^{-1}$)	20	20	?	?
Large herbivores				*
domestic (rel.number in %): cattle, goat	cattle (70) goat (30)	– –	cattle (95–100) goat (1–5)	cattle (95–100) –
game (G): hartebeest, wildebeest, gemsbok, springbok, kudu, ostrich, eland-antelope	G	G	–	–
Land use				*
arable agriculture (rel.area in %)	subsistence**	–	subsistence (1–5) commercial (5–10)	subsistence (1–5) commercial (5–10)
grazing	permanent communal summer grazing	–	fenced paddocks	fenced paddocks
hunting/gathering	subsistence	subsistence	–	–
nature conservation	–	'game reserve'	–	private game reserve + nature reserve (1)
urban	–	–	1	1–5

* considered over West Transvaal as a whole

** presence < 1%

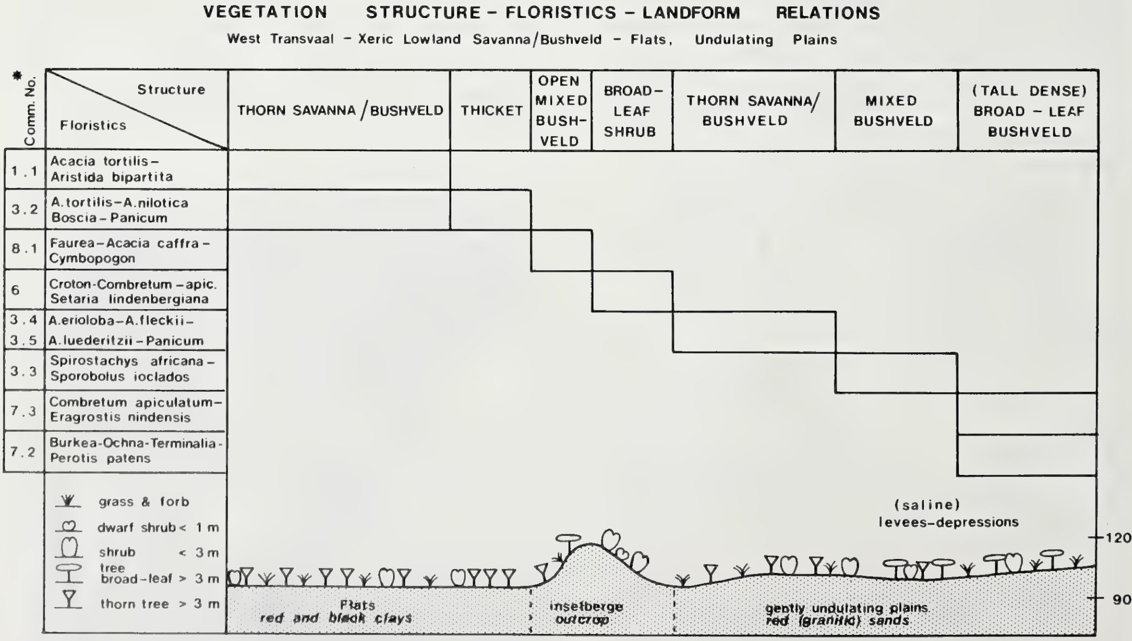
valleys of the Kalahari Basin. The *Acacia* types of the Transvaal survey are described by Van der Meulen (1979) as 'xeric lowland bushveld'. They are common on undulating plains and flats of the Bushveld Igneous Complex Basin. The mesophyllous types are described as 'mesic upland bushveld'. They are usually found on the hills surrounding the Basin, but also in the Basin itself. Floristic community types involved are:- Matsheng: *Acacia erioloba–Acacia luederitzii* Association (Comm. Nrs 7, 8; Fig. 3), Kuhtse: *terminalia sericea–Lonchocarpus nelsii* Association, Nietverdiend: *Acacia*



VEGETATION STRUCTURE – FLORISTICS – LANDFORM RELATIONS

	FLORISTIC COMMUNITIES \ VEGETATION STRUCTURAL UNITS	BARE	DWARF SHRUB LAND	PAN SLOPE GRASSLAND	PAN SHRUB LAND THICKET +/ PAN DUNAL WOODLAND	(PARK) SAVANNA	(SAVANNA) GRASSLAND	OPEN BUSH GRASSLAND	BUSH CLUMP SAVANNA	DENSE SAVANNA/ BUSHLAND	BUSHLAND THICKET
		B									
1	Sporobulus ioclados Composite dwarfshrub		1.1								
2	Rhigozum trichotomum Acacia mellifera		2.1		2.3						
3	Stipagrostis uniplumis Rhigozum trichotomum		3.1	3.2							
4	Acacia erioloba Eragrostis lehmanniana					4.4					
5	Stipagrostis uniplumis Cassia italica						5.5				
6	Aristida stipitatata Stipagrostis uniplumis						6.5				
7	Boscia albitrunca Acacia mellifera							7.6	7.7	7.8	
8	Acacia mellifera Acacia erioloba							8.6	8.7		
9	Acacia erioloba Grewia flava							9.6		9.8	9.9
10	Acacia luederitzii Acacia mellifera				10.3				10.7	10.8	
11	Terminalia sericea Acacia erioloba								11.7	11.8	11.9
12	Boscia albitrunca Cassia italica									12.8	12.9

FIG. 3.—Example of presentation of legend units showing vegetation structure-floristics-landform relations in the Matsheng area of Botswana (CARAP, 1980). Note independence of structure and floristic composition of the vegetation.



VEGETATION STRUCTURE – FLORISTICS – LANDFORM RELATIONS

West Transvaal – Xeric Lowland Savanna/Bushveld – Flats, Undulating Plains

Comm. No.*	Floristics \ Structure	THORN SAVANNA / BUSHVELD	THICKET	OPEN MIXED BUSH-VELD	BROAD-LEAF SHRUB	THORN SAVANNA/ BUSHVELD	MIXED BUSHVELD	(TALL DENSE) BROAD – LEAF BUSHVELD
1.1	Acacia tortilis – Aristida bipartita							
3.2	A. tortilis – A. nilotica Boscia – Panicum							
8.1	Faurea – Acacia caffra – Cymbopogon							
6	Croton-Combretum – apic. Setaria lindenbergiana							
3.4 3.5	A. erioloba – A. fleckii – A. luederitzii – Panicum							
3.3	Spirostachys africana – Sporobolus ioclados							
7.3	Combretum apiculatum – Eragrostis nindensis							
7.2	Burkea-Ochna-Terminalia-Perotis patens							

* Community numbers from Van der Meulen (1979).

FIG. 4.—Example of vegetation structure-floristics-landform relations in the western Transvaal.

erioloba–Acacia fleckii Association (Comm. Nrs 3.4, 3.5; Fig. 4), Nylsvley: *Eragrostis pallens –Burkea africana* Association (Coetzee *et al.*, 1976).

DISCUSSION AND CONLUSIONS

Some conclusions drawn after a comparison of the data (Table 1) are:

Vegetation

The similarity of the vegetation (structure, floristic composition, life form composition) over such a long distance is remarkable when mesophyllous types and microphyllous types are compared, even though differences in rainfall and temperatures occur. In the *Acacia* types, *Acacia erioloba, A. luederitzii, A. mellifera, Boscia albitrunca* and *Rhus tenuinervis* are dominant woody plants. *Rhus tenuinervis* is absent in western Transvaal. Here, *Acacia fleckii, A. tortilis* and *Grewia flava* are common dominants. It is interesting that in the Transvaal survey *Acacia luederitzii* is usually a dominant where *Acacia erioloba* is scarce.

Dominant grasses in the *Acacia* savannas of southern Botswana include various species of *Schmidtia* and *Stipagrostis*. These are infrequent in the Transvaal survey. Here, *Aristida congesta, Eragrostis lehmanniana* and, locally, *Panicum maximum* are the dominants.

The mesophyllous types too have much in common. *Terminalia, Burkea* and *Ochna* are predominant trees. Species of *Combretum* are co-dominant in Transvaal. At Nylsvley, *Grewia flavescens* is a local dominant. *Lonchocarpus nelsii* and *Bauhinia petersiana* (both absent in the Transvaal survey) are dominant trees in the Botswana area. Common grasses in the ground storey include *Eragrostis pallens* and *Digitaria* spp. In western Transvaal, *Eragrostis pallens* is often replaced as a dominant by species of *Diheteropogon* and *Schizachyrium,* tall coarse tufted sclerophyllous grasses indicating mesic conditions.

In all cases, the ground layer mainly consists of perennial hemicryptophytes. Annuals are scarce.

Although life form spectra show great similarity, the height of the trees is positively correlated with increasing precipitation. In the Kalahari area mesophyllous as well as microphyllous trees do not exceed 5–8 m in height. Tree and shrub layers are composed of micro-, nano- and multi-stemmed phanerophytes. Chamaephytes are scarce. In the western Transvaal trees may grow taller, in favourable localities even up to 10–12 m (macrophanerophytes).

Vegetation growth

Savanna growth, from the point of view of large herbivore food (forage), can be subdivided into (i) herbage: forage from herbs (grasses and forbs) and (ii) browse: forage from woody plants (trees, shrubs). An important measure in rangeland survey and management, is forage growth, defined as the increase in forage weight per unit of land and per unit of area. For a given survey area, herbage growth may be predicted from average rainfall applying the following empirical equation (Houerou & Hoste, 1977):

$$y = a + bx$$

where y = forage growth in kg dry matter. $ha^{-1}. yr^{-1}$
x = annual rainfall in mm. yr^{-1}
a = constant (near zero in southern Africa for total dry matter, Walter 1939, Rutherford 1978)
b = constant (4/2 in Karoo-Namib Region for total dry matter; Walter 1939, Rutherford 1978).

From the measured forage growth (CARAP 1980) a rainfall varying between 50–150 mm may be deducted with this formula. Indeed, the survey year (1978/79) was a drought year in the Kalahari: the average forage growth calculated on the basis of the average rainfall (300–400 mm) would be 300–400 gr. m^{-2}. yr^{-1}. However, the surveyor should not use the formula except with great caution. Many other factors may limit forage growth, such as soil fertility, erosion, vegetation composition, fire and drainage. The CARAP survey indicated that forage growth at present does not seem to be the limiting factor for livestock/wildlife production over the Kalahari as a whole.

Because browse data are not known to us from all stations, we concentrate on herbage growth data (above ground standing crop). For the Transvaal, survey area data were only available from Nylsvley Nature Reserve in the northern Transvaal (Huntley & Morris, 1978). These appear to be only slightly higher (90–180 gr.m^{-2}.yr^{-1}; survey years 1974/77) than the data obtained from the Botswana survey (70–160 gr.m^{-2}.yr^{-1}; survey years 1977/78). No data are available from *Acacia* savannas in the western Transvaal. However, no important difference was found between herbage growth of *Acacia* types and mesophyllous types in the CARAP survey (Table 1).

Large herbivores and current land use

As regards land use practices, we concentrate on grazing or browsing by game and domestic livestock. The most striking difference along the transect is in the large herbivores and land utilization types. In the Kalahari, domestic livestock may be locally present (Matsheng, for example), but a rich variety of game is usually found. In the western Transvaal, nearly all the game has been replaced by domestic livestock.

Along the transect land utilization types range from nature conservation and traditional hunting/gathering (Kuhtse) over permanently grazed unfenced communal grazing lands and hunting (Matsheng) to commercial fenced cattle ranches subdivided in paddocks and dry farming of (fodder) crops in the western Transvaal.

The communal livestock grazing lands in the Matsheng area are used also by some of the wild herbivores. It is interesting that, not only the small sedentary browsers (duiker, steenbok etc.) use the grazing land, but also the gregarious larger grazers (hartebeest, wildebeest). The land in the Kuhtse area is a game reserve. Land use envisaged here is tourist viewing. Wildlife utilization is not yet developed in the area.

In the western Transvaal, commercial grazing is the most common type of land use. Ranching is extensive with fenced paddocks and rotation systems. Crop cultivation is practised on a small scale. Irrigated crops are found along some of the permanent rivers. Urban development is still relatively low. However, an increase is expected in the near future, because the area lies at the border of the 'Pretoria-Witwatersrand-Vereeniging Complex', one of the most densely populated industrial areas of the Republic of South Africa. Nature conservation is rarely encountered. Edwards (1974) calculated that less than 1% of Acocks's (1975) veld types involved in the survey area is permanently conserved in conservation areas. On the basis of the western Transvaal survey, representative land units could be recommended for conservation. Game is rare in the western Transvaal. At Nylsvley Nature Reserve, a Provincial Reserve, the following indigenous ungulates were found in decreasing order of importance: impala, duiker, kudu, steenbok, warthog, reedbuck (Huntley & Morris, 1978).

The differences in land use types along the transect are explained by the presence of surface water and the accessibility of drinking water and by the colonization in the last centuries by white pastoralists who knew how to drill wells (Transvaal) and black pastoralists without this knowledge (Botswana).

CONCLUDING NOTES ON SURVEY METHODOLOGY

The examples we have given, show that vegetation should be seen as part of the environment in which other land attributes, like climate, physiography animals and land use also play a role.

Considering the future of small scale vegetation-land use surveys in southern Africa, we recommend integrated surveys of the environment (see Zonneveld *et al.*, 1979). Use of air photo interpretation is indispensable for objective stratified field sampling and to delineate final map boundaries. Field samples are classified into floristic vegetation types according to the Braun-Blanquet tabulation method. Such vegetation types serve as a basis for final map units and are characterized by sociological (or diagnostic) species groups, obtained from the phytosociological table.

The legend units should be presented in an illustrative and ecologically meaningful manner showing the relation between land form, vegetation form (structure) and vegetation composition (floristic types). Examples of such presentation are given in Figs. 3 & 4. It is interesting that the relation between floristically similar, but structurally quite different vegetation types, can also readily be seen from the diagrams. This is important, because structure and composition of the vegetation are often independent (cf. Van der Meulen & Westfall, 1980). Good land unit maps should therefore always have reference to both vegetation form and floristic composition. Presentation of the legend units may also be done in a two- or three-dimensional axis system in which the axes represent the main ecological factors operating in the survey area. Fig. 5 gives an example of such a scheme for the vegetation types which were found in the western Transvaal survey.

In our surveys the 'holistic' landscape approach is adopted. With land surveys of an holistic nature, we mean the study of the environment as an integrated entity that one can study as a whole (Zonneveld, 1979). Final land units are based on an integration of classification of each land attribute of that unit. An important contribution to such an integrated landscape approach in the Republic of South Africa

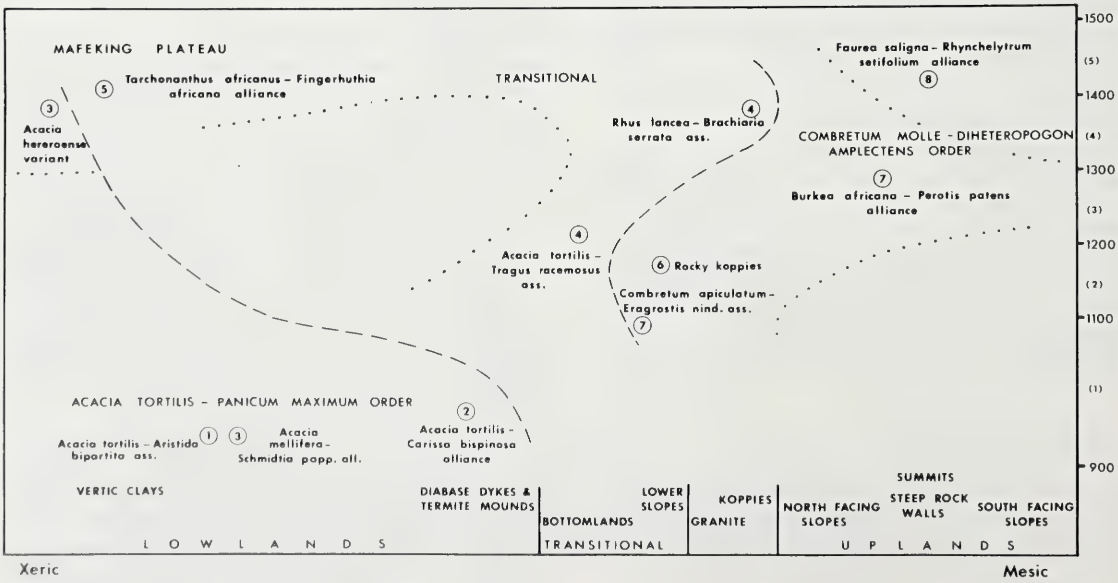

MAFEKING PLATEAU
③ Acacia hereroense variant
⑤ Tarchonanthus africanus – Fingerhuthia africana alliance
TRANSITIONAL
④ Rhus lancea – Brachiaria serrata ass.
• Faurea saligna – Rhynchelytrum setifolium alliance
⑧
COMBRETUM MOLLE – DIHETEROPOGON AMPLECTENS ORDER
⑦ Burkea africana – Perotis patens alliance
④ Acacia tortilis – Tragus racemosus ass.
⑥ Rocky koppies
Combretum apiculatum – Eragrostis nind. ass.
⑦
ACACIA TORTILIS – PANICUM MAXIMUM ORDER
Acacia tortilis – Aristida bipartita ass. ①
③ Acacia mellifera – Schmidtia papp. all.
② Acacia tortilis – Carissa bispinosa alliance
VERTIC CLAYS
DIABASE DYKES & TERMITE MOUNDS
BOTTOMLANDS
LOWER SLOPES
KOPPIES
GRANITE
NORTH FACING SLOPES
SUMMITS
STEEP ROCK WALLS
SOUTH FACING SLOPES
LOWLANDS
TRANSITIONAL
UPLANDS
Xeric
Mesic
1500
(5)
1400
(4)
1300
(3)
1200
(2)
1100
(1)
900
ALTITUDE IN m (HEIGHT CLASS)

FIG. 5.—Major pattern of floristic vegetation types in the western Transvaal in relation to landform, elevation and moisture (from Van der Meulen, 1979).

is the nationwide 'land-type' survey (final mapping scale 1: 250 000) of the Soil and Irrigation Research Institute in Pretoria (MacVicar *et. al.*, 1974). In this physiographic soil survey unit of land with a characteristic combination of relief-type, soil and macro-climate were mapped as 'land-types'. The vegetation of the western Transvaal was mapped on the basis of such a 'land-type' map (Van der Meulen & Westfall, 1979). Clear correlations were obtained between the various land attributes, demonstrating that holistic land units can be arrived at in this way.

Vegetation and land surveys of an integrated nature require a survey team of people from various disciplines, so that various land data can be collected at the same spot simultaneously. Close co-operation between soil and vegetation survey departments is of scientific and economic importance in the survey of natural resources.

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Progress with vegetation studies in South Africa

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ABSTRACT

Vegetation studies at various levels of detail and using various methods are briefly reviewed. The approach and procedures of the Zürich-Montpellier school of phytosociology as a standard methodology for regional studies has become increasingly recognized. Progress has been made in regional studies in the fynbos and woodland biomes, but grassland, forest and karoo vegetation have been much neglected. There have also been marked increases in activity over a wide range of additional vegetation studies including new fields of research, particularly ecosystem studies. However, there are still vast gaps in our knowledge of the basic vegetational resources of the country. A systematic regional-study programme is being launched to remedy these deficiencies in fundamental knowledge.

RÉSUMÉ

PROGRÈS DANS L'ÉTUDE DE LA VÉGÉTATION EN AFRIQUE DU SUD

Les études de la végétation, à divers niveaux de détail et ayant recours à différentes méthodes, sont brièvement passées en revue. La conception et la procédure de l'école phytosociologique de Zürich-Montpellier se sont de plus en plus imposés comme méthodologie classique pour les études régionales. Des progrès ont été réalisés dans les études régionales des biomes du fynbos et de la forêt claire, mais les formations herbeuses, la forêt dense et la végétation du Karoo ont été fortement négligées. Il y a aussi eu une nette augmentation d'activité dans toute une autre gamme d'études de la végétation comprenant de nouveaux champs de recherche, particulièrement des études d'écosystèmes. Cependant, il reste encore de grandes lacunes dans notre connaissance des ressources végétales fondamentales du pays. Un programme systématique d'études régionales est lancé pour remédier à ces déficiences.

Eight years have elapsed since progress with vegetation studies in South Africa was last reviewed at the 1974 AETFAT Congress (Werger & Edwards, 1976). Studies on the vegetation of South Africa have not only increased in number, they have diversified into a wider range of topics and a greater variety of approaches towards the range of topics. In this paper, groups of activities are dealt with in order of generally increasing detail, from general reconnaissance surveys, through reconnaissance and semi-detailed regional studies to larger-scale more-detailed studies, including research on ecosystem function and process, and to problem-orientated studies in the general field of applied ecology, including environmental planning and management. A review of this nature cannot be considered to be complete in that the range of work cannot be exhaustively treated nor can it be fully up to date. References are cited by way of example and do not purport to comprise all the relevant literature.

Reconnaissance and semi-detailed regional studies

The appearance of the second edition of Acocks's (1975) 'Veld types of South Africa' has again drawn attention to the need for revising some of the veld type concepts and of the vegetation map to accommodate resultant boundary changes. Preliminary indications of this need and of Acocks's contribution towards meeting this need were indicated by Acocks (1979). This work was unfortunately interrupted by the passing of Acocks in 1979. Work proceeds slowly on the revision of some 16 veld types of the western part of South Africa as information becomes available from regional studies. Several workers are contributing relevant information (cf. Boucher, 1974 *et seq.;* Gubb, 1981; Le Roux, 1982; Palmer, 1981; Taylor, 1976a & b *et seq.*).

Referring to the previous review, trends noted by Werger & Edwards (1976) have been confirmed. Notable among these is the consolidation of the position of the Zürich-Montpellier approach and methods as a standardized methodology in vegetation surveys. In some cases, the Braun-Blanquet approach and methodology have been used alone; in other cases, they have been used in combination with other methods to provide phytosociological insights that could not have been obtained by using single methods alone.

The programme of vegetation surveys of nature reserves on this basis continues. Other phytosociological studies have also been undertaken outside nature reserves. There is a large and rapidly growing literature which is impossible to review here (cf. Boucher, 1977 & 1978; Boucher & Le Roux, 1981; Campbell *et al.*, 1980; Campbell & Moll, 1976 & 1977; Coetzee, 1975 & 1982; Coetzee *et al.*, 1976; Gertenbach, 1978 & in prep.; Glyphis *et al.*, 1978; Laidler *et al.*, 1978; McKenzie *et al.*, 1977; Taylor, 1981; Taylor & Van der Meulen, 1981; Van der Meulen, 1978 & 1979; Van Rooyen *et al.*, 1981a & 1981b; Viljoen, 1979; Werger, 1980; Werger & Coetzee, 1977; Werger & Ellenbroek, 1980; Westfall, 1981).

Other approaches to regional studies and related vegetation studies at semi-detailed scales have continued along a number of lines that were already being explored prior to 1974 (cf. Werger & Edwards, 1976). A number of these studies may be conveniently grouped under the general heading of remote sensing. Interpretation of conventional air photography is standard procedure in a variety of

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different types of vegetation study and will be referred to again in connection with applied plant ecology in particular. Methodological studies on air-photo interpretation of vegetation cover (e.g. Jarman, 1977) are no longer appearing. This can be taken to indicate the air-photo interpretation is now well established as a tool in sampling strategy, for mapping and for monitoring vegetation change (cf. Drews, 1980a, b & c; Weisser, 1978a & b, 1979b, 1983; Weisser & Marques, 1979; Weisser & Howard-Williams, 1982; Weisser & Müller, 1983; Weisser & Parsons, 1981). The use of satellite imagery is still in the experimental stage and several investigations indicate that there is considerable potential for vegetation and land-use mapping and related studies, and perhaps more especially for monitoring change (e.g. Jarman *et al.*, 1981; Lane, 1980).

Quantitative plant ecology continues to enjoy attention, in that a variety of techniques are applied to a wide range of vegetation studies. Examples includes gradient analysis (e.g. Bond, 1981; Cowling & Campbell, 1981) and multivariate ordination procedures (e.g. Bosch, 1974 & 1978; Theron *et al.*, 1982; Venter, 1976; Westfall *et al.*, 1982) among the more popular quantitative approaches and techniques. Quantitative floristic and structural analyses of vegetation are still being done (e.g. Coetzee & Gertenbach, 1977; Lubke *et al.*, 1976; Moll, 1978a, b & c & 1980a; Rogers & Moll, 1975). In South Africa, the peak of multivariate classificatory methodology, especially experimentation with techniques, appears to have been reached in the seventies (e.g. Kruger, 1974; Morris, 1977; Scheepers, 1975; cf. Coetzee & Werger, 1975b; and Campbell & Moll, 1976). However, clustering procedures and computer manipulation are being used increasingly to speed up phytosociological and other tabulation, and other forms of presentation, while ordination and related techniques are also being used as aids to the interpretation of community/community and community/environment interrelationships (cf. Bredenkamp, 1982; Bredenkamp *et al.*, 1983; Musil *et al.*, 1976; Van der Meulen *et al.*, 1978; Westfall, 1981; Westfall *et al.*, 1982).

Other regional studies

Other more or less pragmatic approaches to vegetation study continue to be used wherever they can be usefully applied in practice as in pasture management and nature conservation for instance (cf. Bredenkamp, 1975 & 1977; Bredenkamp & Theron, 1976; Coetzee & Werger, 1975a; Taylor, 1979; Taylor & Van der Meulen, 1981; Weisser, 1980). Similarly, vegetation mapping continues (e.g. Van der Meulen & Westfall, 1979) where appropriate.

Detailed and specific vegetation studies

Apart from regional studies at semi-detailed scales, other vegetation studies have covered a wide range of activities. Among the more or less floristically based but not necessarily phytosociological studies, mention can be made of more detailed studies mostly of smaller areas, i.e. *not* regional studies. These range in scope from very restricted areas (e.g. Campbell *et al.*, 1980) through areas of intermediate size (e.g. Killick, 1978b) to fairly extensive areas up to the size of regions (e.g. Moll, 1980b; Rogers, 1980). These studies may have no formal phytosociological approach and methodology. Methods are adapted to the limitations of the aims, the size of the area and the scope of the study. There has been continued interest in the structural attributes of vegetation (cf. Edwards, 1983). A noteworthy example of work undertaken to meet a specific need is that of Campbell (Campbell *et al.*, 1981; Linder & Campbell, 1979) who had the task of setting up a structural-functional classification of fynbos to meet the needs of foresters and other land managers to be able to classify vegetation without any botanical training. This classification is particularly required for the management and monitoring of vegetation in mountain catchment areas. A variety of other work can only be referred to in passing here (e.g. Coetzee, 1982; Coetzee *et al.*, 1981; De Moor *et al.*, 1977; Lubke, 1983; Van der Meulen & Westfall, 1980; Van Rooyen, 1978; Werger, 1978). Efforts are being made by Edwards, 1983 (cf. also Campbell *et al.*, 1981) to provide a generally acceptable standardized classification system for South Africa, and possibly for the Southern Hemisphere. Convergence in structure between sclerophyll vegetation types of mediterranean-type climatic regions has continued to excite interest and stimulate work (Cowling & Campbell, 1980).

Recent developments

In recent years, there has been increased interest in diversity as an attribute of vegetation types and floras, much stimulated by the work of Whittaker (1972). Examples of such work are beginning to appear in print (Campbell & Van der Meulen, 1980; Kruger & Taylor, 1979; Whittaker *et al.*, in press). Other work on vegetation attributes includes investigations of pattern (Lubke *et al.*, 1976; Van der Meulen & Morris, 1979; *inter alia*).

Methods and techniques

Papers on methods and their application to South African vegetation have continued to appear intermittently. These range from the aftermath of earlier exploratory methodological investigations (e.g. Campbell & Moll, 1981; Werger, 1977c) to others of a more specialized nature (e.g. Coetzee & Gertenbach, 1977; Rutherford, 1980b; Rutherford & Carr, 1979; Rutherford & Curran, 1981).

Syntheses and theoretical studies

The past few years have seen a number of contributions of a theoretical and abstract nature (e.g. Campbell *et al.*, 1979; Moll *et al.*, 1980). Particularly in evidence have been the number of compilations and syntheses, some of them perhaps somewhat premature (Boucher & Moll, 1981; Brown & Jarman, 1978; Killick, 1978a & 1979; Kruger, 1979; Moll, 1978c; Moll & Werger, 1978; Rutherford, 1978a, 1979c & 1981a; Taylor, 1977b, 1978 & 1980; Walker, 1980 & in prep.; Werger & Coetzee, 1978; White, 1978). These works have been and are being reviewed elsewhere in the open literature and it is not possible to do them justice in this paper. This trend appears to be continuing.

Ecosystem studies and experimental ecology

The most recent and innovative developments in vegetation studies have been in the fields of ecosystem studies and experimental ecology. In terms of extent, utilization and environmental problems, and inherent potential, the Savanna Biome has received priority for multidisciplinary ecosystems research centred on the Savanna Ecosystem Research Site at Nylsvley (Huntley & Morris, 1982; Walker *et al.,* 1978). For similar reasons, as well as for its uniqueness and intrinsic interest as part of the world's biological heritage, the Fynbos Biome Project has also received a high priority for a multidisciplinary approach to function, process and related aspects so as to gain the deeper understanding of fynbos ecosystems needed for their optimal management (Kruger, 1978). Multidisciplinary research programmes are similarly planned for Grassland, Karoo and Forest Biomes. Individual studies contributing to such multidisciplinary research programmes cover a wide range. Regarding the primary producer component, a number of papers have dealt with biomass and productivity (e.g. Cresswell *et al.,* 1982; Grossman *et al.,* 1980; Grunow, 1977; Grunow *et al.,* 1980; Kruger, 1977b; Low, 1981; Rutherford, 1978b, 1979a & b, 1980a, 1981a & b, 1982a, b & 1983; Rutherford & Carr, 1976 & 1979; Rutherford & Kelly, 1978; Rutherford *et al.,* 1978; Steinke & Charles, 1981). Several papers that are more ecophysiological in content are particularly concerned with nutrient relations and water relations (Bate *et al.,* 1982; Bate & Gunton, 1982; Du Preez & Bate, 1981; Furness & Breen, 1980; Henning & White, 1974; Pendle & Bate, 1981; Tew, 1981; Tinley, 1982; Weighill & Walker, 1981; Werger & Ellis, 1981). In some projects, the stage has been reached where there is sufficient information available to allow the commencement of syntheses, particularly the development of mathematical and other models of ecosystem processes. As models are improved, so will it become possible to simulate and predict the changes that will result from manipulating natural and semi-natural ecosystems in various ways (e.g. Morris *et al.,* 1978; Walker *et al.,* 1978; Walker & Noy-Meir, 1982; Walker *et al.,* in prep.; Weisser, 1978c).

Function and process in vegetation are, however, not only being studied at the ecosystem level but also at the species level (cf. Henning & White, 1974). There is increasing interest in phenology and periodicity in vegetation (e.g. Bond, 1980; Steinke & Charles, 1981; Van Rooyen *et al.,* 1979a & b). The interrelationships between form and function, interpreted not only in terms of the environment but also of chorology and population dynamics, are also being studied (e.g. Low, 1980; Mooney *et al.,* 1980; Rutherford, 1980c; Van Rooyen *et al.,* 1980; Werger & Ellenbroek, 1978). The dynamics of South African vegetation have enjoyed a great deal of attention for a number of years and continue to stimulate much research in both basic and applied ecology. Among the more fundamental studies, there are numerous examples of work on dynamics and the monitoring of vegetation change under various conditions and treatments (Downing, 1980; Granger, 1975; Le Roux & Morris, 1977; McLachlan *et al.,* 1980; Robinson *et al.,* 1979; Rutherford, 1981b; Trollope, 1982; Van Daalen, 1981; Walker, 1976; Weisser, 1978b & 1983; Weisser & Marques, 1979; Weisser & Parsons, 1981; Weisser & Müller, 1983; Werger & Leistner, 1975).

Applied vegetation studies

As is well-known, vegetation science has been applied in the fields of nature conservation, pasture science and sylviculture for many years. Recent developments relate to the application of plant-ecological knowledge to environmental planning and management, such as for multiple-use management and environmental impact assessment. The need for this type of work has increased, particularly over the past eight years. This development has been briefly sketched (Van der Meulen & Scheepers, 1978), and broad philosophical and methodological approaches towards meeting this need have been and are currently receiving much attention (e.g. Norton & Walker, 1982; Walker, 1977; Walker & Norton, 1982).

The familiar *ad hoc* or problem-orientated types of vegetation study applied to conservation and reclamation are numerous and only a few examples can be referred to here (Kruger, 1977a; Moll, 1977 & 1980b; Moll *et al.,* 1975; Taylor, 1976a, b & 1977a; Taylor & Morris, 1981; Tinley, 1976; Weisser, 1978a & 1983; Weisser & Ward, 1982). Recent trends in approaches to environmental planning and management, such as environmental impact assessments, can be traced in a growing literature (e.g. Drews, 1980a, b & c; Moll, 1981; Moll *et al.,* 1977 & 1978; Whateley & Porter, 1983; Taylor, 1981a & b; Van der Meulen & Scheepers, 1978; Weisser, 1979a, b & 1980; Weisser & Howard-Williams, 1982). To take one factor of environmental management as an example, the fire factor has continued to receive much attention and a few instances of such work can be cited here (e.g. Downing *et al.,* 1978; Kruger, 1977c; Trollope, 1980; Van Wilgen & Kruger, 1981).

Apart from a rapidly growing literature in the more specialized aspects of pasture science which are not relevant here, several contributions in the general field of applied plant ecology relate to pasture science (Downing, 1974; Fourie & Roberts, 1976; Moll, 1980c; Werger, 1977a, b & d). Similarly, vegetation science is widely applied to vegetation management for sylviculture and the broad field of environmental management (e.g. Taylor & Van der Meulen, 1981; Van Daalen, 1981; Van der Zel & Kruger, 1975). Other applications are assisting towards interpreting the palaeo-ecological environment in archaeological studies (e.g. Moffett & Deacon, 1977).

Summary

General trends that can be discerned include the consolidation of the position of the Braun-Blanquet approach and procedures, mostly in combination with other methods amongst which quantitative methods have continued to figure prominently. Phytosociological and other studies have been pursued in fynbos and woodland (savanna) vegetation, but grassland, forest and karoo vegetation, in particular, have been much neglected. Other approaches and activities include remote sensing using aerial photography and satellite imagery, and vegetation mapping. Apart from floristic composition *per se*, other attributes studied include structure, diversity, pattern, phenology and dynamics. Conceptual analyses and syntheses, applied ecology, mathematical modelling and vegetation monitoring have also received attention. Standardized procedures for veld condition and trend assessment have become part of the stock-in-trade of the pasture scientist and are also being adopted by plant ecologists in basic as well as applied fields of research. Applied plant ecology is being pursued in modern environmental planning and management as well as in the traditional areas of nature conservation and management, pasture science and sylviculture.

These trends can readily be seen at work. Over wide areas, however, there is still an embarassing dearth of basic data about the vegetational resources of the country. To meet the requirement for such basic ecological information, a countrywide inventory of vegetational resources is being launched. This inventory of vegetational resources will be coordinated and integrated with the current survey of other basic natural resources of particular importance to agriculture (MacVicar *et al.*, 1974). To catalogue the resultant information systematically, a standardized system of plant-community nomenclature is required. While much work has been and is being done, there is still ample scope for much more work in the field of vegetation science in South Africa.

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Ecological interpretation of plant communities by classification and ordination of quantitative soil characteristics

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ABSTRACT

An agglomerative cluster analysis and a principal components analysis of habitat, based on 27 quantitative soil variables, are compared with a Braun-Blanquet classification of the vegetation of the Manyeleti Game Reserve in the eastern Transvaal. The results indicate that these techniques can be successfully used to obtain relatively homogeneous habitat classes, characterized by sets of environmental (soil) variables and not only single variables individually, and which are furthermore significantly correlated with the recognized plant communities of the area.

RÉSUMÉ

INTERPRÉTATION ÉCOLOGIQUE DES FORMATIONS VEGETALES PAR LA CLASSIFICATION ET PAR L'ORDINATION DES CARACTÉRISTIQUES QUANTITATIVES DU SOL

Une analyse de groupage par agglomérations successives et une analyse des composantes principales de l'habitat, basée sur 27 variables quantitatives du sol, sont comparées avec une classification suivant la méthode de Braun-Blanquet de la végétation de la Réserve de Faune de Manyeleti dans l'est du Transvaal. Les résultats indiquent que ces méthodes peuvent être valablement utilisées pour obtenir des classes relativement homogènes d'habitats, caractérisées par des ensembles de variables du milieu (sol) et pas seulement par de simples variables considérées individuellement, et qui sont en outre en corrélation significative avec les formations végétales reconnues dans la région.

INTRODUCTION

For the establishment of efficient wildlife management programmes and conservation policies for any area, a sound knowledge of the ecology of the area is an essential prerequisite (Edwards, 1972). It has often been demonstrated that different ecosystems of a particular area can be recognized by the delimitation of the plant communities within the area (Major, 1969; Küchler, 1973; Bredenkamp & Theron, 1978). For this reason, and as part of a vegetation survey programme for conservation areas in South Africa, a study of the vegetation of the Manyeleti Game Reserve was undertaken. Although great diversity and variation occur in the vegetation, there is little conspicuous variation in the topography of the slightly undulating landscape, especially within the relatively small study area. The importance of soil characteristics as a principal ecological factor determining the distribution of plant species and plant communities in the Transvaal Lowveld has been emphasized by, *inter alia,* Van der Schijff (1957), Gertenbach (1978) and Bredenkamp (1982). It has often been shown that the distribution of plant species and, especially, plant communities, is the result of the totality of the present environmental factors rather than of single factors (e.g. Roberts, 1971; D. Scott, 1974; J. T. Scott, 1974; Bredenkamp, 1977).

This paper summarizes the results of an attempt to correlate the plant communities of the Manyeleti Game Reserve to unique sets of soil variables, rather than to certain variables individually. Simultaneously, however, an attempt is made to identify individual variables which could be important for the distribution of the plant communities.

THE STUDY AREA

The Manyeleti Game Reserve, which covers approximately 22 700 hectares, is situated in the Arid Lowveld Veld Type (Acocks, 1975), adjacent to the Kruger National Park, immediately south of the Orpen Gate, between 24°29′ and 24°42′ S and 31°23′ and 31°36′ E (Fig. 1).

The slightly undulating plains of the study area are situated at an altitude of 350–450 m with a slight rise towards the west. Numerous dry drainage lines dissect the area. Archaean granite covers most of the Reserve, but portions of a large dolerite dyke are exposed in the western parts. The soils of the uplands sites on granite are coarse, sandy, acid, leached and dystrophic whereas the soils of the bottomland sites are fine textured, neutral, mesotrophic and calcareous, and sometimes brackish. The soils of doleritic origin are very clayey, alkaline, eutrophic and calcareous.

The climate of the study area is, according to the Köppen index, a BShw climate (Schulze, 1947) where BS = arid steppe climate; h = hot and dry, with mean annual temperature exceeding 18°C; and w = dry winter. The average annual rainfall for the period 1967 to 1979 is 614,6 mm.

Temperatures recorded for Skukuza range from mean daily maximum temperatures of 32,3°C in December and January to mean daily minimum temperatures of 5,6°C in July (Weather Bureau, 1954).

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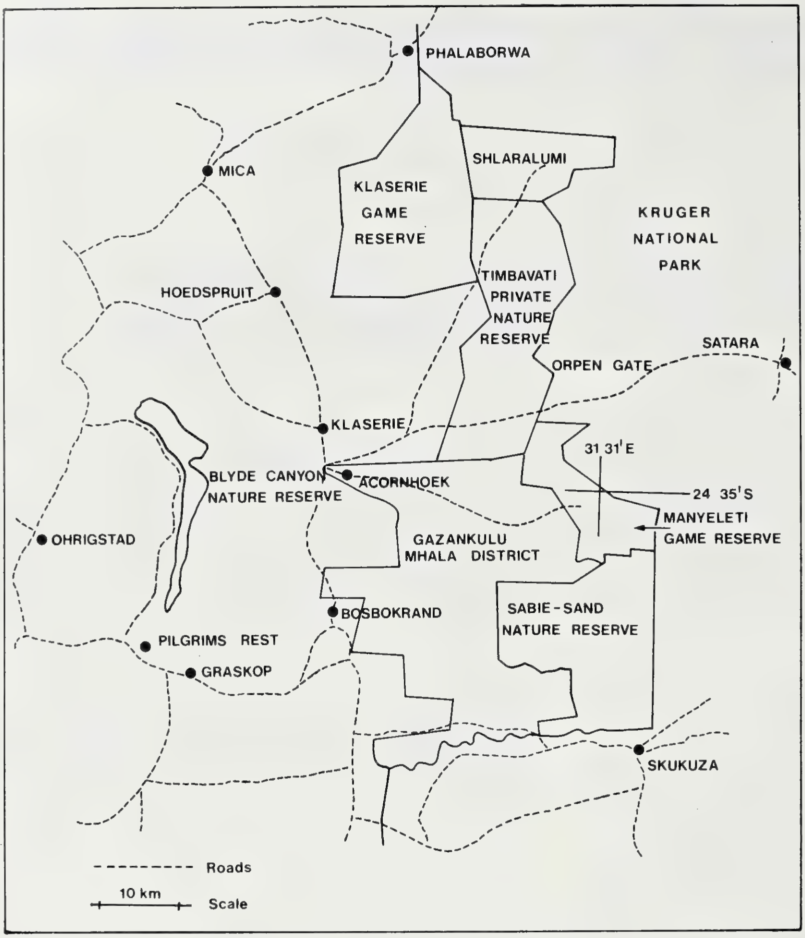

FIG. 1.—Map indicating the position of the Manyeleti Game Reserve.

METHODS

Floristic and habitat data were obtained from 245 stratified random sample plots (Bredenkamp & Theron, 1980).

A Braun-Blanquet analysis of the floristic data from the relevés was carried out independently and before cluster analysis and principal components analysis of soil habitat data (Table 1).

Quantitative data for 27 soil variables were obtained by analysis of soil samples from the 245 relevés (Table 2). The soil variables include:

percentage gravel in the soil sample in the A as well as B soil horizons; percentage coarse sand, medium sand, fine sand, total sand and clay (particle sizes according to MacVicar *et. al.*, 1977) in the A as well as B soil horizons, after the gravel has been removed;

the amounts of exchangeable K^+, Na^+, Mg^{2+}, Ca^{2+} and the S-values (mg/100 g soil) of the A and B soil horizons;

the soil conductivity (u mho/cm) of the A and B soil horizons;

TABLE 1.—The seven plant associations of the Manyeleti Game Reserve (Bredenkamp & Theron, 1980)

Symbol	Association	Habitat
A	*Perotis patens* – *Terminalia sericea* Association	sandy upland granitic soils
B	*Euclea divinorum* – *Acacia nigrescens* Association	black clayey bottomland granitic soils
C	*Themeda triandra* – *Acacia gerrardii* Association	red clayey granitic and doleritic soils
D	*Euclea divinorum* – *Albizia harveyi* Association	black clayey, brackish bottomland granitic soils
E	*Themeda triandra* – *Setaria woodii* Association	black clayey doleritic soils
F	*Cardiospermum corindum* – *Acacia nigrescens* Association	rocky hills
G	*Spirostachys africana* – *Diospyros mespiliformis* Association	river banks

the soil pH (transformed to H^+ ($X10^{-6}$), Haylett (1962), of the A and B soil horizons;

and the soil depth (cm).

Classification and ordination of the habitat were done on standardized data (Seal, 1964) obtained from the absolute quantitative values of these variables.

Classification was done using Orloci's agglomerative cluster analysis (Orloci, 1967) in order to obtain definite and relatively homogeneous habitat classes, based on the variation within the sets of quantitative soil characteristics. This classification was compared

TABLE 2.—Average values for the 27 soil variables in the six soil habitat classes obtained by cluster analysis of habitat data

	Soil variables (A = A soil horizon; B = B soil horizon)	Soil habitat classes					
		CA	CB	CC	CD	CE	CF
percentage	gravel A	9,1	6,8	5,3	0,9	0,8	4,2
	gravel B	42,3	36,5	9,8	2,4	12,6	14,3
	coarse sand A	32,7	26,8	26,8	10,5	9,3	18,5
	coarse sand B	41.0	28,9	25,3	17,7	27,5	24,0
	medium sand A	24,5	22,1	23,0	31,2	10,9	16,4
	medium sand B	22,5	15,0	15,6	33,3	13,7	13,9
	fine sand A	26,7	24,0	24,7	32,6	19,7	23,0
	fine sand B	18,3	16,2	15,8	27,2	17,3	17,5
	total sand A	84,0	73,0	74,7	73,7	37,9	58,2
	total sand B	81,8	60,2	56,5	78,2	58,5	55,6
	clay A	12,8	23,2	20,5	21,8	55,1	35,8
	clay B	15,3	35,0	37,8	18,6	36,3	37,8
	Summary	sandy	clayey	clayey	sandy	very clayey	clayey
mg/100g soil	potassium A	283,8	179,2	189,3	354,4	408,3	337,0
	potassium B	225,0	103,0	101,3	117,6	200,0	193,0
	sodium A	57,7	89,3	107,0	85,3	241,7	122,0
	sodium B	142,6	309,4	385,7	102,9	516,7	204,0
	magnesium A	246,5	538,7	463,3	948,5	4341,7	1545,0
	magnesium B	339,8	1264,9	1136,7	889,7	4683,3	1820,0
	calcium A	190,1	395,8	305,0	1139,7	1958,3	1255,0
	calcium B	128,5	770,8	550,0	580,9	3083,3	1840,0
	S-value A	770,1	1203,0	1065,0	2527,9	6950,0	3556,0
	S-value B	832,4	2447,6	2173,7	1691,2	8481,7	4507,0
	Summary	dystrophic	mesotrophic	mesotrophic	mesotrophic	eutrophic	eutrophic
umho	soil conductivity A	100,7	135,0	150,3	232,6	258,8	212,0
	soil conductivity B	73,8	377,6	1059,7	130,6	1021,3	294,8
	Summary	leached	normal	brackish	normal	brackish	normal
cm	soil depth	108,5	71,7	28,7	88,5	54,0	37,6
	Summary	deep	moderately deep	very-shallow	moderately deep	shallow	very shallow
	pH A	5,6	5,8	5,8	6,7	7,4	7,1
	pH B	6,2	7,0	7,3	7,4	8,2	8,0
	Summary	acid	moderately acid	neutral	neutral	alkaline	alkaline

TABLE 3.—A comparison between the distribution of 245 relevés in the seven Braun-Blanquet plant associations and the six habitat classes obtained by cluster analysis of habitat data

Braun-Blanquet plant associations	Cluster analysis habitat classes (see Fig. 2)						
	CA	CB	CC	CD	CE	CF	Total relevés
A	52	2					54
B	9	20	31	1		1	62
C	4	14	12	1		7	38
D	2	3	32		1	2	40
E					14	9	23
F		2				4	6
G	4	1		15		2	22
Total relevés	71	42	75	17	15	25	245

to and correlated with the seven plant associations of the Braun-Blanquet classification (Table 3).

Ordination by principal components analysis was done to indicate possible gradients in the soil habitat and, by locating the position of each plant assocation in the habitat gradient, it was determined whether or not the associations are restricted to certain areas within the gradient (Table 4). From the results of this ordination, the individual soil variables which could be important with regard to the distribution of the plant communities, were also determined (Table 5).

RESULTS

Classification of the soil habitat by cluster analysis

The dendrogram (Fig. 2) summarizes the results of the cluster analysis. Six soil habitat classes (CA-CF) were obtained at a similarity value of 88%. This high similarity value indicates the relatively small variation in habitat within each class. The average values for each variable in the six classes are given in Table 2.

Comparison of the values of the different soil habitat variables within and between the classes enabled the following soil habitat index to be compiled (for average values and explanation of the terms, see Table 2):

Class CA:	deep, acid, dystrophic, leached, sandy (granitic) soils.
Class CB:	moderately deep, moderately acid, mesotrophic, normal, clayey (granitic) soils.
Class CC:	very shallow, neutral, mesotrophic, brackish, clayey (granitic) soils.
Class CD:	moderately deep, neutral, mesotrophic, normal, sandy (granitic) soils.
Class CE:	shallow, alkaline, eutrophic, brackish, very clayey (doleritic) soils.
Class CF:	very shallow, alkaline, eutrophic, normal, clayey (doleritic soils).

From Table 3 it is clear that the *Perotis patens* – *Terminalia sericea* Association, the *Euclea divinorum* – *Albizia harveyi* Association and the *Spirostachys africana* – *Diospyros mespiliformis* Association are chiefly represented by soil habitat classes CA, CC and CD, respectively. Both the *Euclea*

TABLE 4.—A comparison between the distribution of 245 relevés in the seven Braun-Blanquet plant associations and the seven habitat groups obtained by Principal Components Analysis of habitat data

Braun Blanquet plant associations (see Table 1)	Principal Components Analysis : habitat groups (see Fig. 3)							
	OA	OB	OC	OD	OE	OF	OG	Total relevés
A	50	1	1				2	54
B	4	48	2	5	1	1	1	62
C	2	13	18	3		1	1	38
D		11	5	24				40
E					23			23
F		1			1	4		6
G	1			1			20	22
Total relevés	57	74	26	33	25	6	24	245

TABLE 5.—Eigen values of the soil variables in the first and second components of the ordination

Soil variables (A = A soil horizon; B = B soil horizon)	first component	second component
gravel A	0,398	−0,142
gravel B	0,536	−0,472
coarse sand A	0,707	0,277
coarse sand B	0,568	−0,598
medium sand A	0,685	0,218
medium sand B	0,505	−0,761
fine sand A	0,341	−0,058
fine sand B	0,044	−0,483
total sand A	1,000	0,307
total sand B	0,692	−0,998
clay A	−0,999	−0,316
clay B	−0,686	1,000
potassium A	−0,276	−0,712
potassium B	−0,032	−0,616
sodium A	−0,631	−0,297
sodium B	−0,381	0,900
magnesium A	−0,867	−0,675
magnesium B	−0,841	−0,140
calcium A	−0,810	−0,743
calcium B	−0,749	−0,335
s-value A	−0,903	−0,751
s-value B	−0,878	−0,172
soil conductivity A	−0,546	−0,108
soil conductivity B	−0,374	0,917
soil depth	0,483	−0,748
pH A	−0,721	−0,430
pH B	−0,721	−0,381

divinorum – Acacia nigrescens Association and the *Themeda triandra – Acacia gerrardii* Association are mainly represented by classes CB and CC. The *Themeda triandra – Setaria woodii* Association is restricted to classes CE and CF, whereas the *Cardiospermum corindum – Acacia nigrescens* Association occurs in classes CB and CF.

Concerning the division of the relevés within the soil habitat classes, it is clear that soil habitat class CA is mainly associated with the *Perotis patens – Terminalia sericea* Association, class CD with the *Spirostachys africana – Diospyros mespiliformis* Association, and class CE with the *Themeda triandra – Setaria woodii* Association. Soil habitat class CB is mainly represented in both the *Euclea divinorum – Acacia nigrescens* Association and the *Themeda triandra – Acacia gerrardii* Association, and class CC is also represented in these two associations as well as the *Euclea divinorum – Albizia harveyi* Association. Although the relevés of soil class CF are present in almost all the associations, this class is best represented in the *Themeda triandra – Acacia gerrardii*, the *Themeda triandra – Setaria woodii*, and the *Cardiospermum corindum – Acacia nigrescens* Associations. The statistical chi-square method of Bailey (1974) was used to measure coincidence between the classification of the soil habitat by means of the numerical cluster analysis, based on quantitative soil habitat data and the Braun-Blanquet classification of the vegetation based on qualitative floristic composition. Despite theoretical limitations of the method, the chi-square value of 526,4 (p=0,001 at $\varkappa^2 = 59,7$, 30°f) indicates that the two classifications are indeed highly significantly correlated.

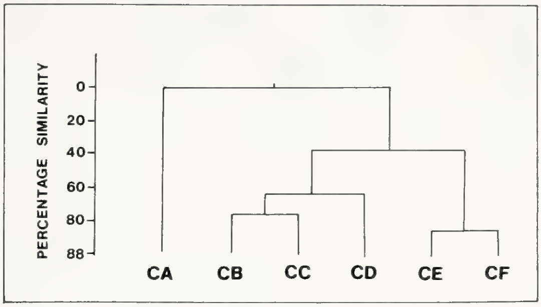

FIG. 2.—A dendrogram indicating the classification of the habitat by cluster analysis.

It may be concluded that the soil habitat classes CA, CE and CD and the *Perotis patens – Terminalia sericea* Association, the *Themeda triandra – Setaria woodii* Association and the *Spirostachys africana – Diospyros mespiliformis* Association respectively, are mutually restricted to one another, within the study area. The soil habitats of the *Euclea divinorum – Acacia nigrescens, Themeda triandra – Acacia gerrardii* and *Euclea divinorum – Albizia harveyi* Associations are fairly closely related (soil habitat classes CB and CC, Fig. 2), at least as far as the measured quantitative soil characteristics are concerned. These three associations occur on mesotrophic clayey soils mainly of granitic origin. Although typical stands of these associations can easily be recognized, transitions in vegetation and habitat are frequently found (Bredenkamp, 1982), which could hamper identification. These transitions (gradients) are also indicated in the results of the ordination which follow.

Ordination of soil habitat by principal components analysis

The results of the principal components analysis of soil habitat data show that the first two components explain 48,9% of the variation in the soil data, and these two components are therefore considered adequate to indicate possible soil habitat gradients and also to show whether there is an associated distribution of plant associations (Table 4).

The arrangement of relevés along the first two components of the soil habitat ordination represents gradients without consistent discontinuities (Fig. 3). Gradients in soil habitat variables (Fig. 3) were established by superimposing the quantitative values of those variables with relatively high eigen values (Table 5) and which contribute greatly to the

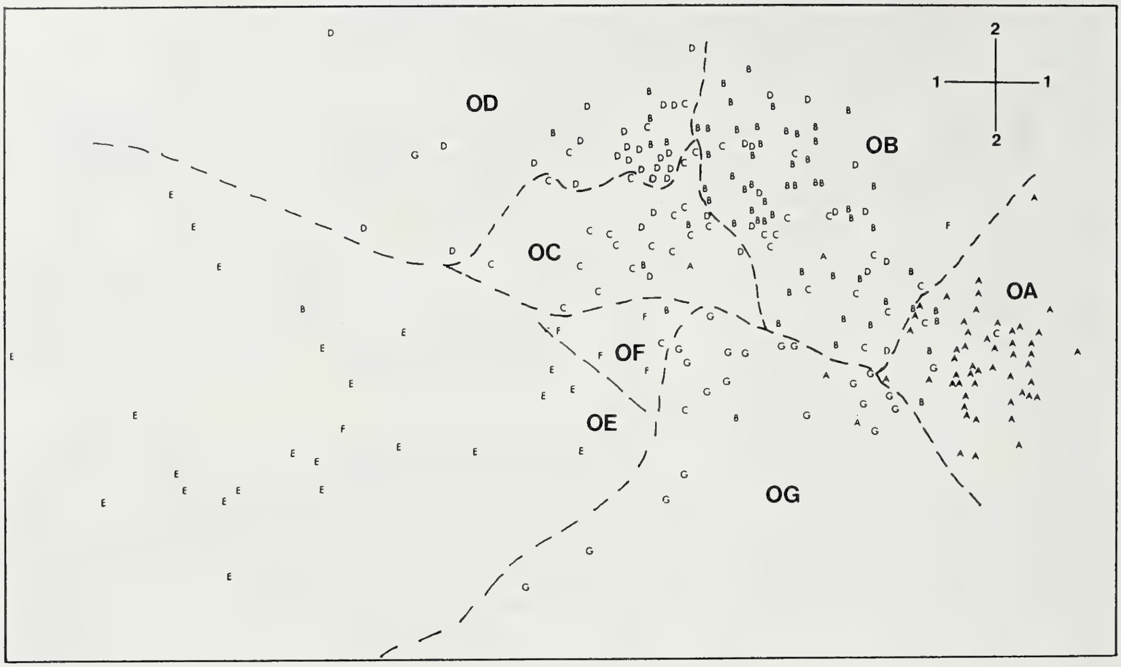

FIG. 3.—The distribution of the Braun-Blanquet Associations in relation to the first and second components of the ordination (Symbols are explained in Table 1.)

distribution pattern of the relevés along the first two components of ordination.

The different Braun-Blanquet plant associations (Table 1), represented by the same relevés than those used in the soil habitat ordination, were superimposed on this ordination and the results (Fig. 3) show that the different plant associations are indeed remarkably confined to certain areas within the soil habitat gradients and consequently the plant associations could easily be delimited (Fig. 3).

The grouping of relevés by principal components analysis of soil habitat data was compared to the Braun-Blanquet classification of these relevés. The results are given in Table 4. From Fig. 3 and Table 4 it is clear that the *Themeda triandra – Setaria woodii* Association is entirely restricted to soil group OE; the *Perotis patens – Terminalia sericea* Association is almost entirely restricted to soil group OA; the *Spirostachys africana – Diospyros mespiliformis* Association to soil group OG; and the *Cardiospermum corindum – Acacia nigrescens* Association to soil group OF. The soil groups OE, OA, OG and OF, furthermore, mainly contain relevés of the abovementioned four assocations respectively. These results indicate that the four groups of the soil habitat and four plant associations are mutually restricted to one another, and largely confirm the results of the cluster analysis.

The *Euclea divinorum – Acacia nigrescens* Association is principally confined to soil group OB (48 of the 62 relevés, that is 77,4%), but group OB also contains relevés from the *Themeda triandra – Acacia gerrardii* and the *Euclea divinorum – Albizia harveyi* Associations. The *Themeda triandra – Acacia gerrardii* Association is mostly limited to groups OB and OC whereas the *Euclea divinorum – Albizia harveyi* Association occurs in group OB and OD. These results indicate, as the results of the cluster analysis, the relationships and transitions between the habitat of the *Euclea divinorum – Acacia nigrescens*, the *Themeda triandra – Acacia gerrardii* and the *Euclea divinorum – Albizia harveyi* Associations.

Despite the somewhat arbitrary delimitations of the plant associations in this ordination, the classification obtained was correlated to the Braun-Blanquet classification by means of the chi-square test of Bailey (1974). The chi-square value of 824,8 (p=0,001 at $\varkappa^2 = 68{,}0$ 36°f) indicates a highly significant correlation between the two classifications.

For each plant association, the average values of the most important variables, i.e. those with relatively high eigen values in the first two components, are given in Figs 4 & 5. Variables with relatively high eigen values in the first component include total sand, coarse sand and clay contents of the A soil horizon and the S-value, magnesium and calcium contents and the pH of both A and B soil horizons (Table 5).

These variables contribute greatly to the distribution of the relevés in the first component. Only the total sand and coarse sand contents of the A soil horizon have positive eigen values and the quantitative values of these two variables mostly increase from left to right, whereas the quantitative

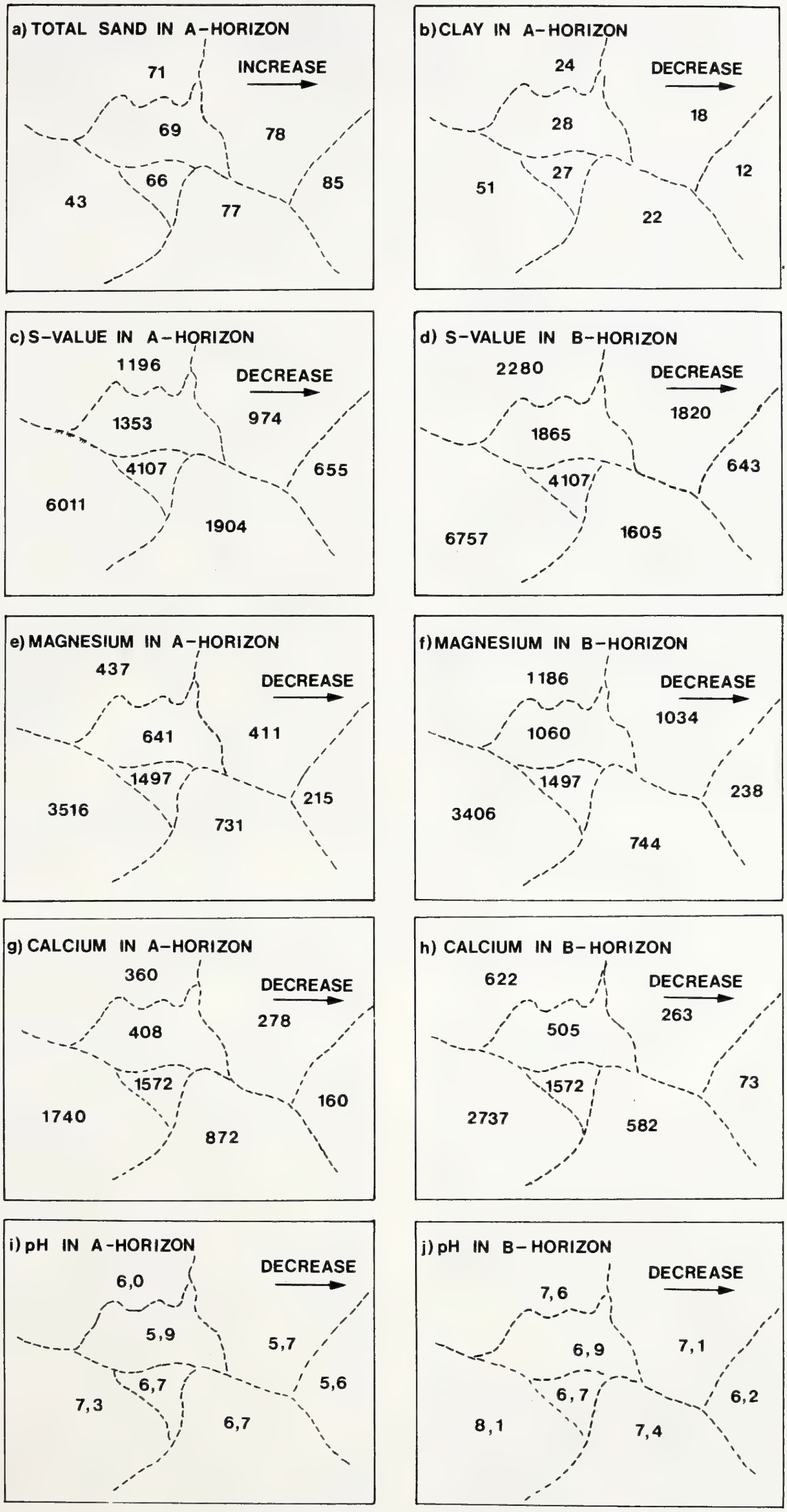

FIG. 4.—Distribution of average quantitative values in each Association of the soil variables with high eigen values in the first component of the ordination.

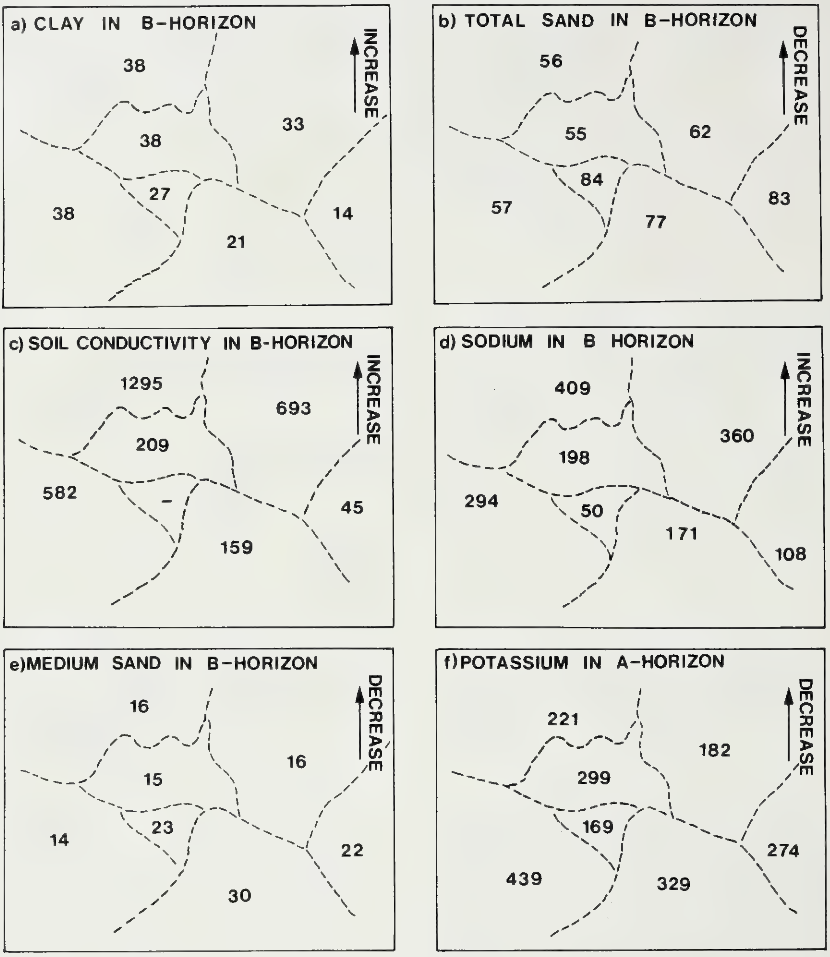

FIG. 5.—Distribution of average quantitative values in each Association of the soil variables with high eigen values in the second component of the ordination.

values of the other important variables mostly decrease from left to right (Figs 3 & 4).

For the second component, variables such as clay content, soil conductivity and sodium content of the B soil horizon are important. With relatively high positive eigen values, the quantitative values of these variables mostly increase from bottom to top in Figs 3 & 5. Variables with relatively high negative eigen values include total sand and medium sand contents in the B soil horizon, calcium, potassium contents and S-value in the A soil horizon and soil depth. The values of these variables mostly decrease from bottom to top (Figs 3 & 5).

According to the zone in the gradients to which the different associations are confined, a suggestion of the relationships of each assocation to the most important habitat variables is made and the transitions between related associations are also indicated. The soil habitat of the *Perotis patens* – *Terminalia sericea* Association is situated at the one end of the soil gradient where it represents acid, coarse, sandy soils, especially low in calcium and magnesium content. This habitat grades mainly into the habitat of the *Euclea divinorum* – *Acacia nigrescens* and *Themeda triandra* – *Acacia gerrardii* Associations with slightly acid to neutral, clayey and nutritionally richer soils, but also, to a lesser degree, into the habitat of the *Euclea divinorum* – *Albizia harveyi* Association which represents the neutral, clayey and mesotrophic but brackish (sodium-rich) soils. The soils of the three last mentioned Associations are closely related and gradual transitions are common. The habitats of the *Themeda triandra* – *Acacia gerrardii* Association and, especially, the *Euclea divinorum* – *Albizia harveyi* Association, also grade into that of the *Themeda triandra* – *Setaria woodii* Association, which is situated at the other end of the gradient where the soils are alkaline, very clayey and eutrophic.

Soils of the *Cardiospermum corindum* – *Acacia nigrescens* Association, which is restricted to the rocky doleritic hills in the transitional areas between dolerite and granite, show relationships with those of the *Themeda triandra* – *Acacia gerrardii* and *Themeda triandra* – *Setaria woodii* Associations. The widely scattered distribution pattern of the relevés of the *Spirostachys africana – Diospyros mespiliformis* Association of the riverbanks (group OG, Fig. 3) indicates the great variation in soil character of this Association. These different soils show relationships with the soils of most other Associations through which the rivers flow. In spite of this variation, these soils could easily be united into a single group (group OG, Fig. 3) which indicate the relationship of these soils to each other.

The results indicate that, although the habitat often represents a complex continuum, soil groups which largely represent the floristic Associations can be established within the gradient.

In conclusion the following can be emphasized:

1. The use of classification and ordination techniques on quantitative soil characteristics proved very successful in obtaining relatively homogeneous soil habitat classes which are (i) characterized by sets of environmental (soil) variables rather than of individual single variables and are (ii) significantly correlated with the recognized plant communities of the area.

2. The soil habitat and distribution of the plant communities were successfully interpreted and the reality of these communities as ecologically significant units emphasized.

3. The transitions in vegetation can also be explained by gradients in the habitat (e.g. Bredenkamp, 1982).

4. Some individual environmental variables which may influence the distribution of the plant communities can also be identified from the results of the principal components analysis.

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Recovery of eastern Cape heathland after fire

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ABSTRACT

In parts of the eastern Cape, fire is increasing in frequency and intensity in heathland, due mainly to the presence of adventive exotic tree species. These adventives also smother the indigenous vegetation under a dense canopy or with leaf litter. This heathland flora requires a long period to reach its climax and under present conditions, this is rarely attained.

RÉSUMÉ

RECOUVREMENT DE LA LANDE DU CAP ORIENTAL APRÈS LES FEUX

Dans certains régions orientales de la Province du Cap, la fréquence et la force des feux qui détruissent les bruyères s'accroissent, causes surtout par la présence d'espèces d'arbres exotiques. D'autre part, ces intrus étouffent la végétation indigène sous un dôme de verdure et ils sont également nuisibles par la litière de feuilles. Il faut très longtemps à la flore indigène pour retrouver son climax et ceci arrive très rarement maintenant.

INTRODUCTION

Heathland occurs continuously in southern Africa from the western Cape to the Great Fish River in the eastern Cape (Acocks, 1975). Thereafter isolated areas of heathland are found at high altitudes on, for example, the Drakensberg of Natal and Lesotho (Killick, 1963; Jacot Guillarmod, 1971) and up into Ethiopia (see Fig. 4.1 in Killick, 1979). In the Cape Province it is found from sea level to mountain tops wherever soil and climatic conditions are suitable. This vegetation type is now endangered over most of its range in the Cape Province because of man's demands for more agricultural and pastoral land (Trollope & Booysen, 1971) and also the spread of invasive exotic tree species. Fire is also a serious threat to maintenance of species diversity and existence of heathland. Due to the presence of many adventives, mainly woody, fire is an increasing hazard both in intensity and frequency.

STUDY AREA

Eastern Cape heathland exists mainly on Witteberg quartzite-derived soils. These are acid and usually well drained. This soil type extends for only a short distance, as isolated spurs of the Suurberg range, north-eastward beyond the Great Fish River (Fig. 1). It is rarely now that any species typical of heathland can be found in this easternmost portion, now in the Ciskei in a heavily populated area. This vegetation type, described by Acocks (1975) as False Macchia (Type 70) or as nanophanerophyte shrub heathland by Martin & Noel (1960) can therefore be considered extinct beyond the Great Fish River, that is, the easternmost extent of its former distribution within the boundaries of the Cape Province at the time Acocks made his survey of vegetation types of South Africa.

On the south-eastward side of the Great Fish River, heathland is still to be found on the Suurberg range and other outcrops of Witteberg quartzite. The present study area (Faraway) is situated at 33°20'S, 26°29'E and rises to 700 m a.s.l. (Fig. 2). A comparable area of heathland, studied by Martin (1965) for primary communities and plant succession and later, also by Martin (1966) for the effects of burning, lies nearby. This is the Grahamstown Nature Reserve, situated at 33°20'S, 26°31'E. Both plots face south, are on spurs of the Suurberg range and have the same heathland type of vegetation. The Grahamstown Nature Reserve is approximately 81 ha in extent, while the study plot is 31 ha. Both areas have been subjected to fire at irregular intervals and while the Grahamstown Nature Reserve has been kept almost entirely free of invading exotic tree and shrub species, the study area was, in 1974, almost completely covered by these. The species found were *Pinus* spp. (mixed in origin but basically of *P. pinaster* or *P. halepensis*), *Hakea sericea, Acacia longifolia, A. saligna,* and *Solanum mauritianum.* From August 1974, the area was steadily cleared of such exotics so that by August 1980, it was free of these except for a narrow belt along the south-western boundary (Fig. 2), where some very large trees stood.

By growth ring counts and from photographic evidence, it was estimated that the average age of the great majority of the pine trees was 15–17 years; the much larger, older trees were at least 45–50 years old and some may have been even older. Photographs taken in the early 1960's showed an extensive heathland with a scattering of young pine trees only just above the level of the heath vegetation, and a few massive large trees. Though some of the very old trees may have been planted, the younger growth was self-sown or adventive. The cover of trees over the heathland was dense and light penetration was very poor. Leaf litter was deep reaching one metre in a few places where it had settled against obstructions. Etiolated *Protea cynaroides* had produced weak stems three metres in length, projecting up through pine tree branches but many of these were dead stems. Only where an opening, due to fallen trees, existed, could remnants

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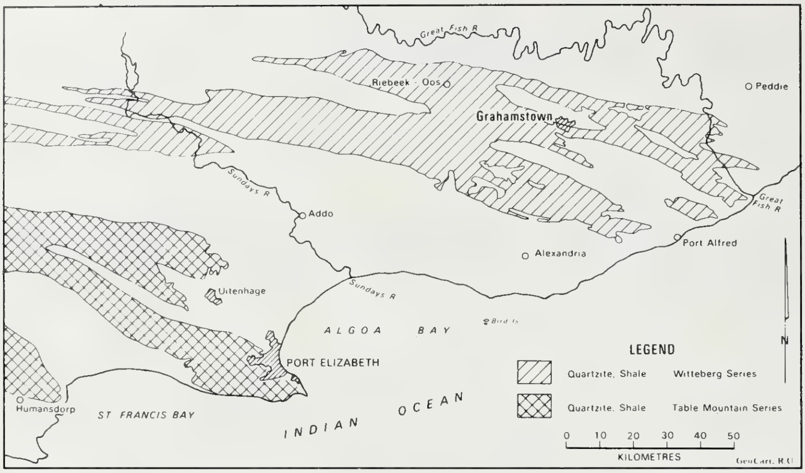

FIG. 1.—Witteberg and Table Mountain series quartzite occurrences in the eastern Cape and Ciskei (east of the Great Fish River).

of the heathland flora be found but even here *Erica chamissonis* bushes were usually dead. Species diversity was low and much of what was present was not flowering.

CLIMATE

The eastern Cape is on the border of the summer and winter rainfall region, along the coastal strip; it experiences a variable precipitation. On average, near the Great Fish River the rainfall is 380 mm or less per annum, but on the spurs of the Suurberg (where the two areas, Grahamstown Nature Reserve and the study plot) are situated, rainfall is higher. A six-year record kept on the study plot gives an average of 850 mm a year. Fog must add considerably to the moisture available to plants in both areas. A mist meter has only recently been installed and data are not yet reliable. Frost seldom occurs and is never severe but snow may fall and lie during winter (Jacot Guillarmod, 1980). The prevailing wind is southwesterly.

METHODS

During the six years preceding August 1980, and as the indigenous vegetation recovered from the effects of the pine tree cover, a record was kept of species identified. Specimens were placed in the Albany Museum Herbarium, Grahamstown (GRA). This record of regenerating heathland was not complete when a fierce fire, fanned by a very strong and dry northwesterly wind ('berg wind'), swept across the study area on August 23rd, 1980. The previous six months had been particularly dry for the area (Table 1) and all vegetation was therefore especially subject to fire damage; even leaves of succulents were wilted or drying up. During the six hours of active fire passage (the wind though mainly north-westerly, veered and backed, so that trees which had escaped the first flames, were later burnt), all live plant material on the heathland was consumed. The marginal trees of the forest patch were also burnt; these were *Rapanea melanophloeos, Apodytes dimidiata* and *Zanthoxylon capensis* for the most part. Only the small portion of

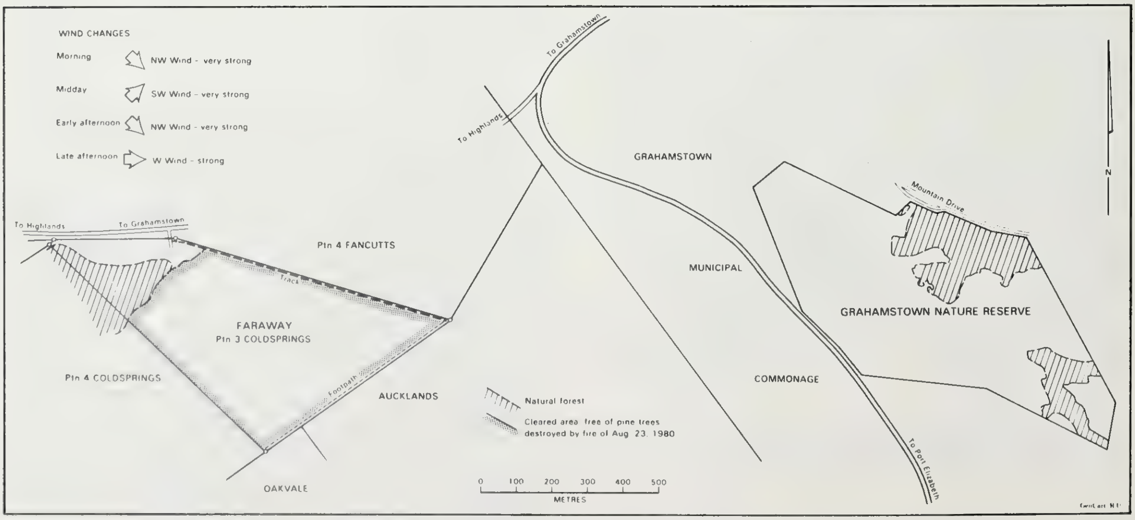

FIG. 2.—Study plot and its relation to Grahamstown Nature Reserve.

heathland lying above the forest escaped destruction. Stumps of previously cut pine trees and underground roots continued to burn on the area for several days after August 23rd.

After the fire, a record of species regenerating was begun; this included time of flowering, date of recognition from characteristic growth form (e.g. *Schizaea pectinata*), height at flowering, and extent of cover, etc. With the detailed work of Martin (1966) for comparison, it should be possible to establish the time taken for this particular type of heathland to reach what Martin considers its climax form, dominated by *Erica chamissonis* and *E. demissa.*

TABLE 1.—Precipitation and temperature data for study area. Faraway

Climatic factor and period	Data
Average annual precipitation on study plot (6 years)	860 mm
Precipitation for six months preceding August 23rd, 1980	184 mm
Precipitation during sixteen days following fire of August 23rd, 1980	
August 26/27	5 mm
August 31/ Sept. 1	8 mm
Sept. 1/2	4 mm
Sept. 6/7	24 mm
Sept. 7/8	4 mm
Totals during three months following fire	
Sept.	75 mm
Oct.	59 mm
Nov.	66 mm
Temperature on day previous to fire (August 22nd., 1980)	max. 29,5°C min. 17,5°C

RESULTS

Regeneration after the fire in August 1980 was assisted by favourable weather conditions. The warmer weather of the spring season was accompanied by gentle rain at frequent intervals. Sufficient plant cover had grown before the first heavy rain storm so that erosion was minimal on the exposed slope and seed had good conditions for germinating. Table 1 gives the main points for climatic conditions.

The first plant to flower was *Cyrtanthus angustifolius* (commonly known as 'fire lily'). The first flower was open by August 30th. The flower stems preceded the leaves and within six weeks more than 300 of these plants had flowered. A second group produced vegetative growth first, and within a month, were flowering; this included *Senecio concolor* and *Clutia heterophylla.* A third group, characterized by *Bobartia macrocarpa* and the grass, *Alloteropsis semialata,* were in flower within three months of the fire. A fourth group of plants has taken a year to reach the flowering stage and includes woody shrubs and trees (e.g. *Halleria lucida*) and biennials *(Senecio pterophorus)* which have appeared from seed that germinated after the fire. Some species, recorded as present before the fire, had not been noted as present fifteen months after the date of the fire. These include seed regenerating species such as *Erica chamissonis* and several other *Erica* species, where the seed requires to be blown into the area by wind from some outside source. It also includes the fern, *Gleichenia polypodioides.*

Seed regeneration has lagged behind regeneration from underground perennating organs in this study area. Only 9% of species noted has proved to be from seed germination, whether from seed present in the area and unaffected by fire (or stimulated, as with *Acacia longifolia,* from supplies dormant previously) or from introduced seed in the post-fire period. All exotic weeds noted for the area prior to the fire have reappeared as seedlings, with one exception, *Hakea sericea. Senecio concolor* has regenerated not only from stock but also from seed apparently blown into the area. Bond (1980) suggests there may be various barriers to seed distribution. One barrier in this case is the lack of seed supplies from other areas, as the fire destroyed heathland on most of the surrounding hillslopes and in the valleys.

DISCUSSION

Martin (1966), in comparing the previous state (Martin 1965) of heathland with post-fire regeneration, established five groups of appearance of plant species — flowering within a week, within a month to five weeks, within three months, within a year, and lastly, the species requiring seed supply from stocks outside the burnt area. The present study area has demonstrated this grouping for the first four sections, and the period since the fire has not been long enough to establish whether the fifth group will re-appear. Martin also states that species in this fifth group take at least eight to ten years to become fully established and to produce the climax state of eastern Cape heathland.

Bond (1980) working in senescent fynbos (heathland) in the Swartberg area of the southern Cape, has indicated that too long an interval between burning may also lead to reduction in species diversity. His experimental areas included 40–50 year old heathland and mature heathland of 18–20 years. The present study area could perhaps be considered as approximately six years old (1974–1980) prior to the fire, and approaching its climax, as *Erica chamissonis* was becoming a dominant. The previous dense cover of pine trees had acted to suppress the natural species diversity, which was regenerating when the fire burnt the area.

Acocks (1975) considers heathland took over from temperate forest as the climate of southern Africa became drier and Von Breitenbach (1972) also indicates the destruction of forest encourages the extension of heathland. However, fire at too frequent intervals reduces the diversity of species in heathland and, where these are present, increases the number and variety of exotic weed species whether by stimulating germination of seed already present (*Acacia* species) or by the rapid germination and growth of introduced seed on exposed areas.

This present note will be followed by a more detailed account of the recovery of the study area but, at present, Martin's conclusions for the Grahamstown Nature Reserve seem to be valid for eastern Cape heathland. Specimens of material collected are being placed in the Albany Museum Herbarium, Grahamstown (GRA) together with notes, and plots are being studied regularly by other workers.

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A broad-scale structural classification of vegetation for practical purposes

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ABSTRACT

An *a priori* system is presented for the broad structural classification of vegetation. The objectives are to provide a descriptive, consistent, easily applied system, with unambiguous, straight-forward terminology, which can be used in the field and with remote sensing and air photo techniques, and which can be used in conjuction with floristic and habitat terms to convey the essential physiognomy and structure of the vegetation. The attributes used are a primary set of four growth forms, a set of four projected crown cover classes, and a set of four height classes for each growth form. In addition, shrub substratum is used to define thicket and bushland. Special growth forms, substratal, leaf and other attributes can be readily incorporated to extend the two-way table system where such detail is needed.

RÉSUMÉ

UNE CLASSIFICATION STRUCTURALE À GRANDE ÉCHELLE DE LA VÉGÉTATION À BUT UTILITAIRE

Un systéme a priori *de grande classification structurale de la végétation est présenté. Son but est de fournir un système descriptif, logique et d'application aisée, avec une terminologie directe et sans ambiguïté, pouvant être utilisé sur le terrain et avec des techniques de télé-détection et de photographies aériennes, et pouvant être utilisé conjointement avec des termes de floristique et d'habitat pour traduire la physionomie et la structure essentielles de la végétation. Les éléments utilisés sont: un ensemble de quatre formes biologiques, un ensemble de quatre classes de recouvrement (projection des cimes) et un ensemble de quatre classes de hauteur pour chaque forme biologique. En plus, la sous-strate arbustive sert à définir le fourné et la formation buissonante. Des formes biologiques spéciales, des caractères de la sous-strate, des feuilles et autres peuvent aisément être incorporés pour étendre le système du tableau à double entrée, lorsque cela se justifie.*

INTRODUCTION

Recognition of the different structural kinds of vegetation are as old as man himself and is etymologically rooted in words such as forest and thicket in languages over the world. In the purely structural sense, such different kinds of vegetation have been significant for the activities of man from the hunter and food gatherer stage to the modern technological phase. In modern botanical literature, physiognomic-structural classifications of vegetation date chiefly from the latter part of the last century (see e.g. Mueller-Dombois & Ellenberg, 1974; Dansereau, 1957; Kuchler, 1967; Beard, 1978, 1981) with a resurgence of interest since the advent of the International Biological Programme (IBP) in the late 1960's when comparison of the vegetation for different parts of the world was needed. Notable systems of classification proposed at this time were that of Fosberg (1967), which was suggested for use by the International Biological Programme and was based upon purely vegetational attributes, and that of UNESCO by Ellenberg & Mueller-Dombois (1967), which was based upon vegetational structure and physiognomy as well as broad ecological attributes. As a result of work done for the IBP, it became evident that certain difficulties were encountered in the application of the Fosberg system, and independent strikingly similar modifications were proposed in the three southern hemisphere countries of Australia (Specht, 1974; 1981), Brazil (Eiten, 1968; 1972) and South Africa (Edwards, 1976, unpublished).

This contribution is presented since it is evident that there is still a need, at least locally, for a simple, consistent, broad-scale classification of vegetation for a variety of purposes ranging from needs in natural resource inventory, vegetation description, remote sensing, air photo interpretation and mapping, to needs from other non-plant scientific disciplines. Although the structural classification proposed here is in line with similar recent classifications, it differs in certain basic concepts and in some of the terminology which at a broad scale is more uniformly applicable, but where such detail is needed can also take into account local kinds of specialized vegetation by using specialized terms. The structural classification is regarded as purely complementary to and independent of floristic and other forms of vegetation classification and may be useful on its own for certain purposes. It is restricted here to terrestrial vegetation dominated by predominant angiosperm, gymnosperm and pteridophyte plant growth form types. For purely practical reasons, of observation and description, it is limited to the above ground portions of vegetation.

1 BASIC CONSIDERATIONS

As defined by Danserau (1957), *vegetation structure* is 'the organization in space of the individuals that form a stand (and by extension a vegetation type or a plant association)' and the 'primary elements of structure are growth-form,

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stratification and coverage'. Although, as discussed by Mueller-Dombois & Ellenberg (1974) and Barkman (1979), there are other usages and interpretations of vegetation structure, the definition of Dansereau is used here as a working definition that includes spatial as well as morphological features of vegetation, but excludes purely floristic features. In accordance with Fosberg (1967), 'physiognomy is the appearance, especially the external appearance, of the vegetation, partly resulting from, but not to be confused with, *structure* and *function* . . . .'.

As pointed out by Fosberg (1967), a distinction should be made between classifications of vegetation based solely on the properties of the vegetation itself and those based also on various environmental factors, which are more properly termed ecological classifications and in which care must be taken to avoid circular reasoning leading to false correlation. The structural classification proposed here is based solely on vegetation characters and is independent of, but complementary to, floristic, habitat and ecological classifications of vegetation.

Since growth form, cover, height and other attributes that qualify the various structural characteristics of vegetation show continuous variation, vegetation is viewed here as a multi-dimensional continuum that may be segmented at certain arbitrarily defined points to provide a classification, which is an abstraction. Although discontinuities may exist in any particular region, elsewhere intermediates will usually be found so that the abstract class limits are essentially a matter of convenience in conformity with general usage and acceptance. For purposes of description, communication and understanding, definition and classification are necessary, bearing in mind the oft forgotten corollary that classifications are abstractions in which a certain range of internal class variation ('heterogeneity') is found dependent on the classificatory level and fineness of resolution (approximate to the concrete level) that is intended.

Although the *a priori* kind of classification is often rejected on the grounds of unreality and that knowledge is inadequate for proper definition, this is only true if the classificatory criteria are irrelevant or are such that they do not cover the range of possibilities within the purpose of the classification. For the finer resolution of the more detailed levels of classification, *a priori* classifications may well prove inadequate because of the lack of knowledge needed to adequately define these more detailed levels, but this does not preclude the validity of *a priori* classification at the broader classificatory levels where such fine information is not necessary. The intention here is to provide a definition of the broader structural classes of vegetation so that they may convey a more precise and consistent meaning to these structural kinds of vegetation.

Terminology is an important but difficult aspect of the structural classification of vegetation. Once one proceeds beyond a simple set of binomials or trinomials, terminology becomes a clumsy diagnostic description rather than a terse, usable, specific phrase. An endeavour has been made here to provide a set of simple consistent, basic terms for the broader structural classes of vegetation, as well as in the consistent appropriate use of terms for certain common parameters of vegetation, for example, cover and density. As an expression of the percentage of the ground surface that is covered by plants, cover may more realistically be referred to as closed, open or sparse rather than as dense and mid-dense. The latter usage can only serve to confuse when referring to a high or moderate density of plants, which is expressed in either the spacing or the number of plants per unit area and for which density is the standard and universally recognized term. Confusion is further enhanced by an older common use of dense canopy when this refers to the thickness or light impedance of the canopy, which at least has some merit.

2 BASES OF THE STRUCTURAL CLASSIFICATION

The proposed structural classification is hierarchical and at the levels considered here is based on a set of dominant primary growth form types, cover, height and partly on substrata. Further subdivision, on leaf character, leaf permanence, subsidiary growth form types, etc., are not considered here.

The primary attributes used in the structural classification are, therefore,

- a primary set of four growth form types,
- a primary set of four cover classes and
- a set of four height classes for each growth form type.

In addition, shrub substratum has been used to define a thicket and bushland class, which is considered necessary at this stage, and a set of desert vegetation classes below a certain total plant cover.

The basic procedure followed to determine the structural classes is to establish a matrix or two-way table as follows:

(1) Growth form × cover = structural group,
(2) Structural group × height = formation class.

The ranking terms structural group and formation class that will be used here are tentative.

2.1 *Primary growth form set*

Four types of growth form are considered as being the primary set of attributes that determine the essential spatial geometry of vegetation. These are self-supporting plant growth forms, which are grouped into four main classes, namely, woody trees and shrubs, and non-woody grasses (and graminoids) and herbs, defined as follows:

Trees are rooted, woody, self-supporting plants over 2 m high and with one or a few definite trunks normally branching above ground level;

Shrubs are rooted, woody, self-supporting plants up to 5 m high, multi-stemmed and branching at or near ground level when 2–5 m high, or either multi-stemmed or single-stemmed when less than 2 m high;

Grasses are rooted, non-woody, herbaceous plants belonging to the family Poaceae, or graminoid plants, such as Cyperaceae and

Restionaceae, resembling grasses. At lower levels of classification, Cyperaceae and Restionaceae would be referred to specifically as sedges and restioids. Although members of the Poaceae, many bamboos are best considered as trees or shrubs, or as bambusoids at lower levels of classification;

Herbs are rooted, non-woody, self-supporting, non-grass-like plants. If woodiness is evident, this is restricted to the permanent lower portions of the plant at or near ground level.

Woody lianes and herbaceous climbers are considered either as shrubs, herbs, or grasses (if grass-like or Poaceae) when growing in the absence of other supporting plants, or as subsidiary defining growth forms for lower classificatory levels.

Trees, shrubs, grasses and herbs are further subdivided on height (2.3).

2.2 *Cover classes*

Cover is defined in the accepted sense as the vertical projection of the crown or shoot area of the plant onto the ground. Unless otherwise stated, cover here refers to the projected crown cover. The cover of the upper growth form stratum is basic to the structural class definition and refers to the total canopy cover (out of 100%) of that growth form, irrespective of differences in height class (see Fig. 1). In this way, the problem of defining a 'dominant' tree or other layer is avoided when there is considerable variation in height of the primary growth form stratum.

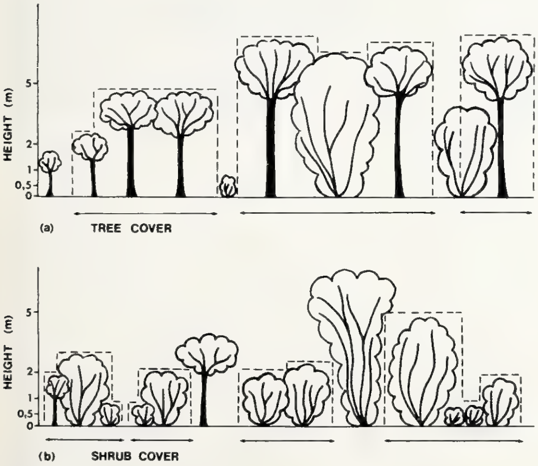

FIG. 1.—Basis of canopy cover determination illustrated (a) for trees and (b) for shrubs. Note in (a) and (b) shrub over 5 m high classed as tree and in (a) and (b) tree less than 2 m high classed as shrub.

Although normally given as a per cent of the ground reference, cover may also be expressed in other ways, such as the dimensionless crown: gap ratio, given in terms of the ratio of mean crown diameter to the mean distance, as number of crown diameters, between the crowns of the plants. Thus, with reference to a hexagonal closest packing of circular crowns before overlapping, the percentage crown cover is given by $\frac{90,7}{(n+1)^2}$ where n = the mean number of crown diameters by which the plant crowns are separated (see Fig. 2). Similarly, for a somewhat looser square packing of crowns the formula is approximately $\frac{80}{(n+1)^2}$. The method has been independently derived by Eiten (1968) and Edwards (1976), but crown:gap ratios have been used by various authors such as Ellenberg & Mueller-Dombois (1967), Boughey (1957); Fosberg (1967), Tinley (1969) and others. It is important to note that cover as estimated by the crown:gap ratio is based on a ground projection of the crown as a whole, whereas many other cover estimates are based on estimates of foliage cover (e.g. Specht, 1974), which will be lower for species with open foliage crowns. The projected crown cover is more consistently and easily estimated, especially on vertical air photos, than the projected foliage cover. It is also possible to relate by photographs or other estimates the projected crown cover to foliage cover for different species.

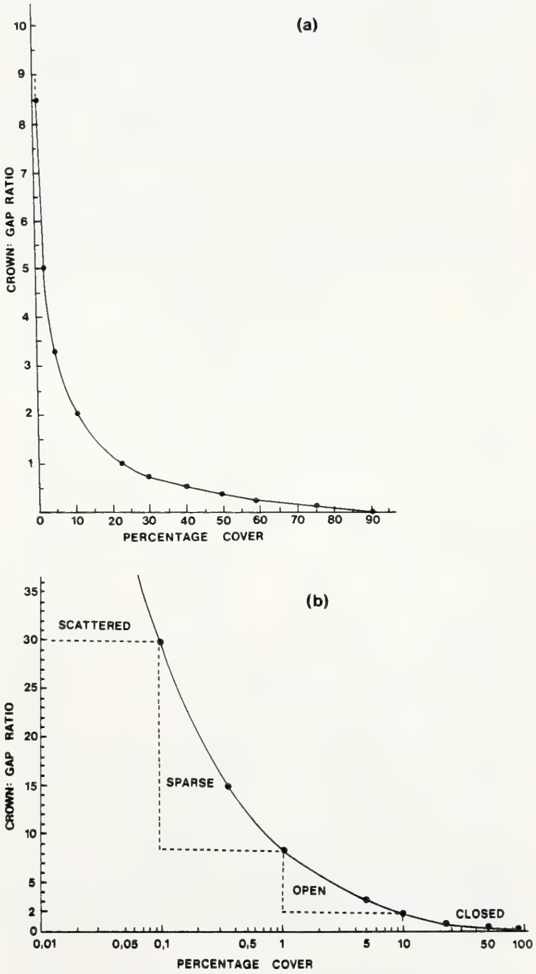

FIG. 2.—Relationship of crown:gap ratio to percentage cover (a) linear scale and (b) semi-log scale. Primary cover classes with crown:gap ratios shown in (b).

The method is useful in air photo interpretation and also shows other interesting features (Fig. 2). When the crown diameters are known, density can be quickly estimated in terms of the spacing between individuals. It is also evident that for a specific percentage cover, the smaller the crown diameter the higher the density, so that normally for a specific plant cover shrublands have higher plant densities than woodlands. Furthermore, at a cover of 25% the crown to gap ratio is 0,9, whereas at 10% the ratio is 2, showing that despite the apparently low per cent cover the spacing between individuals is closer than may be expected for these relatively low percentage cover values. Light interception even at a cover of 10% is likely to be appreciable, especially with increasing plant height and increase in latitude. As shown by Rutherford (in press) in the Northern Transvaal bushveld, root spread for *Burkea africana* may be some seven times greater than the canopy diameter, so that root competition between individuals, even at what appears as a low canopy cover of 10%, is intense and, in certain plant communities at least, is not unexpected if the spacing is taken into account. From a functional view point it therefore seems appropriate to lay greater stress on class separation at the lower end of the percentage cover scale by considering the espacements of plants as related to cover instead of the purely areal cover percentages of plants. For these reasons, preference is for a logarithmic approach to the basic cover class intervals used in the classification (Table 1).

TABLE 1.—Primary and subsidiary cover classes

Primary cover classes			Subsidiary sub-divisions		
Cover	% Cover	Crown:Gap	Cover	% Cover	Crown:Gap
Closed	10–100	0–2	Continuous (Overlapping or nearly so)	76–100	<0,1
			Sub-continuous	51–75	0,1–0,3
			Moderately closed	26–50	0,3–0,9
			Semi-open	11–25	0,9–2,0
Open	1–10	2–8,5			
Sparse	0,1–1	8,5–30			
Scattered	<0,1	>30			

As shown in Table 1, the terms attached to these cover classes have specific meanings. Although not used here, except for 75–100% overlapping cover in the case of trees, there is often a requirement for finer subdivision of the wide range of percentages in the closed cover class. It is suggested that the subsidiary subdivisions as shown in Table 1 be used which, apart from terminology, are as suggested by Campbell *et al.* (1981).

2.3 *Height classes*

Height classes used for the different primary growth form types are shown in Table 2 and, for reasons similar to those discussed for cover (2.2), are logarithmic in character. The term height class is used as distinct from stratum, since height class is essentially an arbitrary circumscription whereas stratum refers to a natural layering of the vegetation provided by one or more growth forms, or a certain height layering of a growth form. A height class 'tall tree', for example has a definite meaning in terms of metres above ground and may cut across natural height strata, whereas a 'tall' tree stratum may include several tree height classes, or may straddle two height classes.

TABLE 2.—Height classes

	Trees	Shrubs	Grasses & herbs
High	<20m	2–5m	>2m
Tall	10–20m	1–2m	1–2m
Short	5–10m	0,5–1m	0,5–1m
Low	2–5m	<0,5m	<0,5m

As shown in Table 2, for different growth forms the same terms in the same order show increasing height, the height ranges being similar for shrubs, grasses and herbs. The high tree, high grass and high herb classes as well as the low shrub, grass and herb classes are given as open-ended but could also simply be extended into extra classes, for example, 20–50 m for trees, 2–5 m for grasses and herbs, 0,2–0,5 m and 0,1–0,2 m for shrubs, grasses and herbs if required.

It must be appreciated that, based on sufficiently extensive sampling, any given set of height classes will never be universally 'natural' and will apply better in one vegetation type than in another. What is given here is, therefore, an arbitrary but meaningful height terminology for vegetation based on certain commonly but by no means universally accepted height standards. It is suggested that where an obvious stratum straddles two height classes this be indicated by a '/' between the two height classes, bearing in mind that the actual height range will obviously be recorded in the detailed description.

When determining the dominant height class that describes the height of a structural group, it must clearly be realized as to which part of the growth form stratum the term is applied. Based on cover and height, a definition of the dominant height class that is simple and leads to the fewest anomalies is as follows:

Within a closed or open growth form stratum the dominant height class is the tallest height class whose cover is greater than, equal to, or not more than one cover class less than the cover of any lower height class. For a sparse or scattered (desert) growth form stratum the dominant height class is simply a conspicuous taller height class.

For example, for a particular growth form stratum, an open cover height class above a closed cover height class will be recognized as the dominant height class, but not a sparse cover height class above a closed cover height class when the closed height class would be recognized as the dominant height class. A sparse cover height class would be the dominant height class when above an open, sparse, or scattered lower height class.

3 THE STRUCTURAL CLASSIFICATION

As derived from combinations of the sets of growth form, cover and height attributes, with a limited use of substratum growth form to define Thicket and Bushland and of total plant cover to define desert vegetation classes, the structural classification is set out in Table 3 and is further illustrated diagrammatically in Fig. 3, which illustrates the intergrading character of cover and height of the dominant growth forms and the segmenting of this continuum.

Table 3 is self-explanatory, being essentially a multiple entry key to the nine structural groups A–I, which are Forest and Woodland, Thicket and Bushland, Shrubland, Grassland, Herbland, Desert Woodland, Desert Shrubland, Desert Grassland and Desert Herbland. Each structural group is then subdivided on the basis of the height of the dominant height class, as defined in 2.3, into 72 formation classes. The Desert structural groups are separated initially from the non-desert groups on the basis of total plant cover.

A certain measure of additional complexity has had to be introduced into Table 3, because of the need to define a Thicket and Bushland structural group in relation to Forest and Woodland on the basis of the shrub stratum, which has had further to be qualified in terms of height in relation to tree height. This is necessary to specify the continuity in height and cover of trees and shrubs that characterize Thicket and Bushland formation classes. A similar exception to the logical simplicity of Table 3 has also had to be introduced in the case of Closed Shrublands where there is present a sparse tree cover over a tall closed shrub cover. This has been considered necessary because of the closely related character of short and low trees and high and tall shrubs. In general, further attention is to be devoted to the incorporation of substratal characteristics into the classification but, in the meantime, except for Thicket, Bushland and Closed Shrubland as defined, it is suggested that where there is a high substratal cover in relation to the dominant defining growth form of the structural group the terms 'shrubby', 'grassy' and 'herby' be used.

Despite what may appear as complexity in Table 3, the classification is actually extremely simple and easily memorized. All that is needed is understanding of the simple procedures for cover and height determination, the easy memorization of the growth forms, cover and height classes, and of the three qualifications for Thicket, Bushland and Closed Shrubland. The class limits and terminology are simple, logical and consistent.

The classification proposed here is most similar to those of Specht (1974, 1981) and Eiten (1968, 1972) and to a lesser extent Fosberg (1967), but differs markedly in a number of features. The chief difference is in the use here of projected crown cover rather than of projected foliage cover. However, in the latter use, higher cover values are used to separate classes than here, so that the difference is not as marked as would appear at first sight since projected foliage cover is usually lower than projected crown cover. Use of the subsidiary cover classes given in Table 1 to subdivide the broad closed cover class used here would bring this classification more closely in line with many other classifications insofar as cover limits are concerned. To do so would be simple and straight forward without further modification to Table 3.

More overall attention is here given to cover at the lower limits than for other classifications. The distinction of sparse classes of woodland and shrubland, which in the absence here of any other substratal or co-dominant (possibly even dominant in the functional sense) recognition other than the suggested shrubby, grassy or herby at present, may well raise comment (cf White, In press). However, the general use of a sparse tree cover over a closed grass layer, for example, is often useful for certain ecological situations, such as dynamic ones, where an invasion of grassland by trees is taking place as a result of disturbance by human activity. Recognition of the class is in the structural sense demarcation of the continuum from woodland to grassland. Provision is, therefore, made for sparse formation classes of vegetation but qualification is recommended as previously indicated. For regional mapping sparse woodland, for example, would often be mapped in association with grassland.

Finally, in terms of the criteria for classification as given by Whittaker (1978), the structural classification given here appears to be: (i) highly accessible in that the community attributes used are simple and readily observable on the ground and from the air; (ii) the criteria are significant at the broad classificatory level in distinguishing the broad structures of vegetation and in covering the

TABLE 3.—Tabular key to structural groups and formation classes

Dominant height class	*Total plant cover > 0,1%*				*Total plant cover ≤0,1%*
	Total tree cover >0,1% shrub cover <10% if >1 m high **A. Forest & Woodland** *Total tree cover*				**F. Desert woodland** *Trees dominant*
	100–75% *0–0,1ø*	*75–10%* *0,1–2ø*	*10–1%* *2–8,5ø*	*1–0,1%* *8,5–30ø*	
Trees >20 m	1. High forest	5. High closed woodland	9. High open woodland	13. High sparse woodland	57 High desert woodland ?
Trees 10–20 m	2. Tall forest	6. Tall closed woodland	10. Tall open woodland	14. Tall sparse woodland	58. Tall desert woodland
Trees 5–10 m	3. Short forest	7. Short closed woodland	11. Short open woodland	15. Short sparse woodland	59. Short desert woodland
Trees 2–5 m	4. Low forest	8. Low closed woodland	12. Low open woodland	16. Low sparse woodland	60. Low desert woodland
	Total tree cover >1% shrub cover >10% & >1 m high **B. Thicket & Bushland** *Total tree cover*				
	100–10% 0–2ø		*10–1% 2–8,5ø*		
Trees 5–10 m & shrubs 2–5 m	17. Short thicket		19. Short bushland		
Trees 2–5 m & shrubs 1–5 m	18. Low thicket		20. Low bushland		
	Total tree cover <0,1% shrub cover >0,1% or tree cover up to 1% & shrub cover >10% & >1 m high (closed shrublands) **C. Shrubland** *Total shrub cover*				**G. Desert shrubland** *Shrubs dominant*
	100–10% 0–2ø	*10–1% 2–8,5ø*	*1–0,1% 8,5–30ø*		
Shrubs 2–5 m	21. High closed shrubland	25. High open shrubland	29. High sparse shrubland		61. High desert shrubland
Shrubs 1–2 m	22. Tall closed shrubland	26. Tall open shrubland	30. Tall sparse shrubland		62. Tall desert shrubland
Shrubs 0,5–1 m	23. Short closed shrubland	27. Short open shrubland	31. Short sparse shrubland		63. Short desert shrubland
Shrubs <0,5 m	24. Low closed shrubland	28. Low open shrubland	32. Low sparse shrubland		64. Low desert shrubland
	Total tree cover <0,1% shrub cover <0,1% grass cover dominant and >0,1% **D. Grassland** *Total grass cover*				**H. Desert grassland** *Grasses dominant*
	100–10% 0–2ø	*10–1% 2–8,5ø*	*1–0,1% 8,5–30ø*		
Grasses >2 m	33. High closed grassland	37. High open grassland	41. High sparse grassland		65. High desert grassland
Grasses 1–2 m	34. Tall closed grassland	38. Tall open grassland	42. Tall sparse grassland		66. Tall desert grassland
Grasses 0,5–1 m	35. Short closed grassland	39. Short open grassland	43. Short sparse grassland		67. Short desert grassland
Grasses <0,5 m	36. Low closed grassland	40. Low open grassland	44. Low sparse grassland		68. Low desert grassland
	Total tree cover <0,1% shrub cover <0,1% herb cover dominant and >0,1% **E. Herbland** *Total herb cover*				**I. Desert herbland** *Herbs dominant*
	100–10% 0–1ø	*10–1% 2–8,5ø*	*1–0,1% 8,5–30ø*		
Herbs >2 m	45. High closed herbland	49. High open herbland	53.High sparse herbland		69. High desert herbland
Herbs 1–2 m	46. Tall closed herbland	50. Tall open herbland	54. Tall sparse herbland		70. Tall desert herbland
Herbs 0,5–1 m	47. Short closed herbland	51. Short open herbland	55. Short sparse herbland		71. Short desert herbland
Herbs <0,5 m	48. Low closed herbland	52. Low open herbland	56. Low sparse herbland.		72. Low desert herbland

Note: (1) % cover refers to projected crown cover as percentage
(2) ø refers to mean crown: gap ratio as mean number of crown diameters apart
(3) where straddling of height classes occurs this may be indicated by '/'
(4) where mosaics of classes are found this may be indicated by '//' e.g. High closed // open woodland
(5) where there is a high substratal cover of shrubs (excluding thicket & bushland as defined), grasses, or herbs, this may be indicated by terms such as 'shrubby', 'grassy' and 'herby'

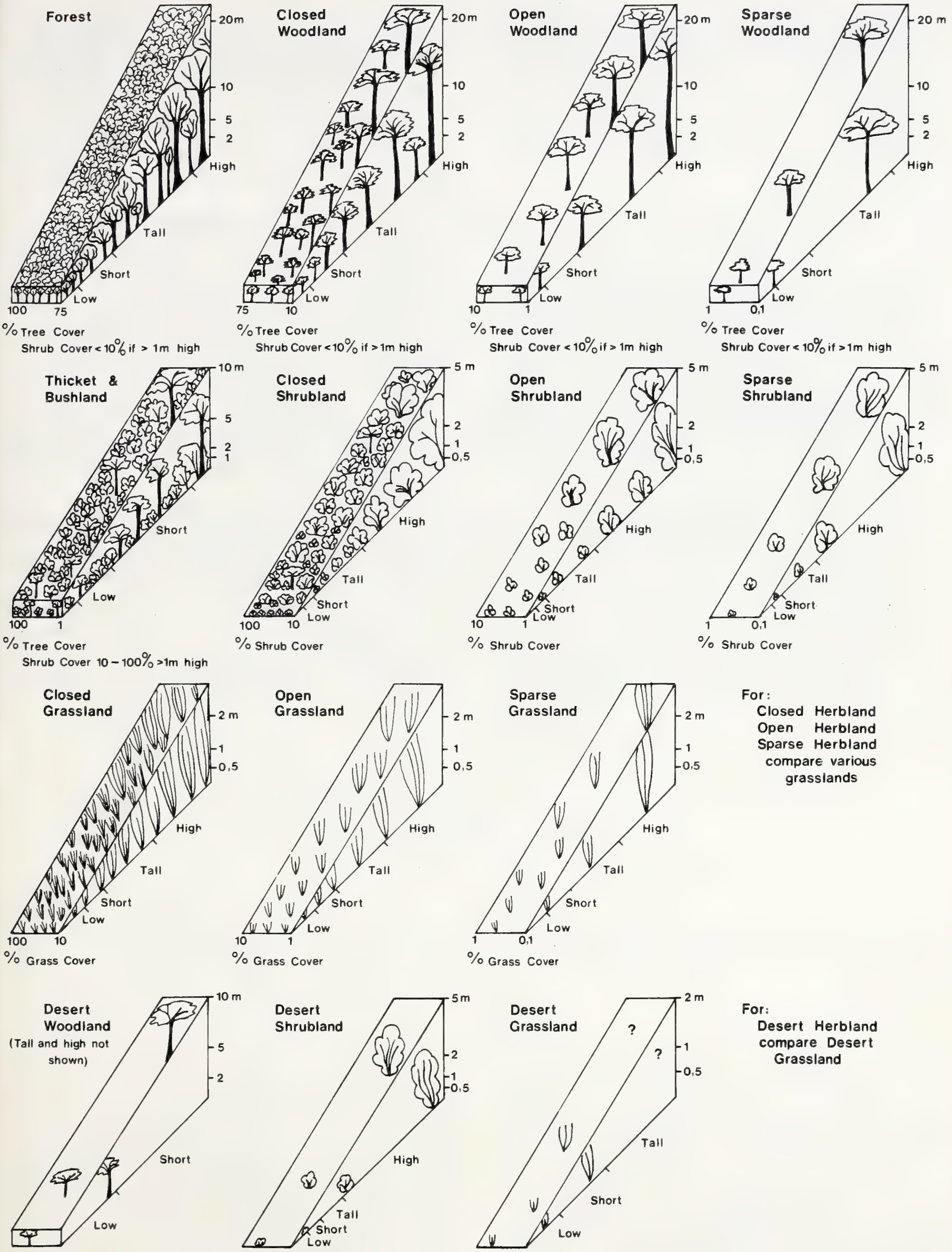

FIG. 3.—Diagrammatic representation of structural groups and formation classes. Dominant growth forms only are shown.

continuum from forest to desert in all combinations of primary growth form type, cover and height; and (iii) effective at the broad scale of resolution, but also, as field trials have shown, remarkably sensitive to structural differences in vegetation at the local scale. Assessment of effectiveness can, however, only be judged by extensive use and on the basis that no one approach to a structural classification can claim exclusive merit.

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A contribution to the concept and the classification of the bioclimatic unit in Sub-Saharan Africa

J. F. V. PHILLIPS*

ABSTRACT

A bioclimatic unit is an integration of climatic factors (e.g. radiation, humidity complexes) and features modified by physiography and vegetation (biotic communities and associated habitats, i.e. wherever possible, ecosystems).

Unit implies an entity irrespective of ecological status and dimensions: these are otherwise differentiated.

It often must suffice to use vegetation communities, because information regarding biotic communities or ecosystems is unavailable.

Increasingly, disturbance of 'natural' conditions makes it imperative to involve man in the classification, demarcation and policy for the development of bioclimatic units.

Ignorance regarding the nature and distribution of a climax necessitates using pro- (pre- or post-) climaxes.

This is based upon the differentiation in these criteria: climatic (radiation and humidity complexes); vegetation (physiognomy and ecological status) . . . and as these are further modified by physiography and edaphic features (physiognomic differentiation ranges from specific faciations of forest or thicket); wooded savanna (facies of woodland, shrubland); facies or faciations of grassland; climatic differentiation ranges from highly humid to arid . . . and further to subdesert and desert.

Recommendations respecting policy and practice in pastoral, crop production and forestry development based on this concept have been used in various sectors of Africa. South East Asia and Latin America. Detailed experience has been gained in Natal and elsewhere.

Several maps illustrate the application of the concept.

RÉSUMÉ

CONTRIBUTION AU CONCEPT ET À LA CLASSIFICATION DE L'UNITÉ BIOCLIMATIQUE DE L'AFRIQUE AU SUD DU SAHARA

Une unité bioclimatique est un complexe de facteurs climatiques (par exemple radiation, humidité) et de données modifiées par la physiographie et la végétation (les biocénoses et leur milieu, c'est à dire, chaque fois que c'est possible les écosystèmes).

L'unité bioclimatique est une entité indépendante de tout status écologique et de toute de dimensions; ceux-ci sont différenciés d'une autre manière.

Souvent on doit se limiter aux formations végétales faute d'informations sur les biocénoses ou les écosystèmes.

De plus en plus, la perturbation des conditions 'naturelles' nous oblige tenir compte de l'homme dans la classification, la délimitation et le plan de développement d'unités bioclimatiques.

L'ignorance en ce qui concerne la nature et le répartition d'un climax nécessite l'emploi de pro- (pre- ou post-) climax.

La différenciation des critères du climat et de la végétation ont servi de base à la définition des unités bioclimatiques.

Les recommendations quant à la politique et à la procédure pour le développement des pâturages, de l'agriculture et de la foresterie, basées sur ce concept, ont été appliquées dans divers secteurs d'Afrique, du Sud-Est asiatique et d'Amérique latine. Une expérience approfondie a été acquise au Natal et ailleurs.

Plusieurs cartes illustrent l'application de ce concept.

DEFINITION OF A BIOCLIMATIC UNIT

It is impracticable to discuss the history of the concept of bioclimatic units here. Even the UNESCO-FAO Working Party (1963), responsible for a series of bioclimatic maps of the Mediterranean Zone, did not attempt this. Space-consuming without being gainworthy in practice, this must await a wider opportunity.

Because this Working Party achieved a noteworthy success in producing a series of scientifically sound and practical maps, it is fitting to record its concept that the purpose of a bioclimatic map is to exhibit, for a particular region, a synopsis of the climatic factors of special importance for living creatures. In practice, the Working Party was essentially concerned with the interreplay of climatic factors and vegetation.

My concept of a bioclimatic unit is that of a natural region wherein influent climatic factors, as modified by physiographic features and edaphic conditions, control the growth and welfare of vegetation so as to permit its development to a stage where this is in dynamic equilibrium with the climate.

A more satisfactory ecological definition would introduce *biotic* communities rather than vegetation

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but, because of the preponderant emphasis in practice, on vegetation, I have perforce acquiesced. Although the climatic climax is inherently involved in this definition, in practice it may be expedient to work with proclimaxes or other penultimate communites.

OBJECT

What is the purpose of presenting a summary of the concept and classification of my bioclimatic studies in Sub-Saharan Africa, published more fully elsewhere (Phillips, 1959, 1961, 1966) and applied to specific purposes (Phillips, 1965, 1968, 1970)?

My purpose in working on the subject during the decade ended in 1959 is as applicable today as thirty years ago, i.e. a desire to provide an ecological background for the guidance of those responsible for selecting habitats suitable for the satisfactory production of annual or perennial crops; pastoral conditions and livestock; conservation and management of wild animals; and the conservation and silvicultural management of indigenous forests and species, as well as the possible role of selected exotics. To grosser experience gained in Sub-Saharan Africa and parts of S.E. Asia and Latin America have been added, during almost two subsequent decades, opportunities in southern Africa for application of the concept and associated practice on scales still relatively extensive, but yet demanding finer detail and additional criteria.

Humbly, I believe that in the still developing countries in the tropical to subtropical continents, the concept and discipline are capable of helping the cause of sound ecological criteria and bases becoming more effectively involved in the selection, development and management of aptly selected projects for the production of renewable natural resources.

To give some background to the anxiety of an octagenarian, may I record that in several continents during the decade subsequent to the placing of the East African Groundnut Scheme on a 'pilot' basis, my experience with international, state and other individual enterprise made clear that it would be fairly long before ecological criteria would mean much to developers of terrain on a large scale in the farflung vegetation of Africa and elsewhere in the tropics. Although some signs of improvement appear from time to time, the overall challenge still remains strident, hence my endeavour to draw attention, once again, to the necessity of infusing more ecological understanding into political and administrative circles and into the citadels of the developers of agricultural and related projects.

METHODS OF APPROACH

During the years of my endeavour to obtain climatological, vegetational, pedological and other edaphic information adequate to my requirements for drafting a bioclimatic map and a supporting text, there was not yet a modern vegetation map (Keay's AETFAT work appeared in late 1959); nor comprehensive climatological maps (Jackson's atlas was published in 1961); nor was D'Hoore's S.P.I. map of the major soil groups completed until 1964.

Despite these serious lacks, there was a varying amount of information, both published and other: British, German, French, Belgian, Italian, Portuguese, of older and more recent vintage, and American. This, much collaboration and visiting of such examples of the terrain as I could possibly arrange, formed the basis for my admittedly simple and crude attempts at synthesis of map and text.

It behoves me to note one outstandingly useful publication by the notable French forester-ecologist, M.A. Aubréville (1949), Inspecteur Général des Eaux et Forêts des Colonies which, together with other papers and the author's interest, from time to time, proved invaluable, mainly in West Africa.

From various sources I was able to collect and collate climatological data (various parameters of temperature, vapour pressure, saturation deficit, rainfall, potential evapotranspiration, ecologically dry months, drought periods during the seasons of precipitation), to correlate with vegetation communities of major extent and signifance. This information was summarized in tabular form in the text (Table 1). Walter (1955; 1958) had not yet published the useful technique of climatic diagrams, the calculation of which would have given a greater precision to subdivisions of the bioclimates.

At the reduced scale at which the map (Fig. 1) had to be produced (1: 20 million), it was essential to adopt a limited number of growth forms of vegetation for description. A summary follows:

Forest

Forest may be evergreen to mixed evergreen and in some instances partially and temporarily deciduous; 18–60 m tall, with crowns touching, overlapping or almost so, to stratified so as to create a closed to almost closed canopy. Tree, shrub, fern, forb and other layers may number 3–5 or more, but from some types ferns may be wholly absent. In some types, the general top canopy may not be formed by the tallest emergent trees, which form a higher, very much more open canopy. Epiphytes and lianas vary greatly in kind and density. This physiognomic community is frequently climax, but may often be associated with successional stages such as thicket, woodland and wooded grassland, mostly secondary in origin. Only rarely to occasionally are the species of trees relatively restricted in number, but more commonly they are numerous.

Thicket

Thicket may be evergreen to wholly or partially deciduous; the height may range from 10–24 m, the stems may be branched or clear; the trees and taller shrubs are often closely spaced, with stems clear; the trees and shrubs are often closely spaced, with stems and crowns intertwined.

Derived savanna

A general term relating to woodland, open woodland, wooded grassland and thicket secondary to forest into which various elements of wooded savanna vegetation have entered in the course of

TABLE 1. – A general comparison of climatic factors conditioning the major bioclimatic regions of the tropics and subtropics of Sub-Saharan Africa, with notes regarding extent and degree of disturbance (Phillips 1957, 1959, 1961, *et seq.*)

Map symbol Bioclimatic region	Temperature °C mean shade	Humidity and saturation deficit : mb	Rainfall : mean annual mm	Drought : ecologically dry months : edm*	Extent and degree of disturbance
1. HHF : highly humid forest, low and medium elevations, equatorial and subequatorial	Megatherm : +23° C range very slight annual and daily	+27–20–27, sat. deficit 1 – below 4	Above +2500; 1800–2500: regular	Nil to rare; edm : 0, rarely 1–2	Shifting cultivation locally extensive, edaphic factors moderately to severely deteriorated
1/5. Swamp forest and HHF in Congo	Similar to 1	Similar to 1	Similar to 1	Similar to 1	
1-16. HHF being converted to derived wooded savanna : relics numerous	Essentially as for 1, except for aerial changes caused by extensive disturbance of forest canopy	Somewhat less humid than 1	Similar to 1	Similar to 1	Shifting cultivation, steadily removing forest relics – open woodland on increase, edaphic factors deteriorating
2. HF : humid forest low and medium elevations, equatorial and sub-equatorial	Megatherm : +23° C but above 750–900 m meso-megatherm 20–22° Range slight/very slight annual and daily	20–27, sat. deficit 4–7, to 4–1	1800–2500 (to 1400–1800); regular to moderately regular	Short-mild, rare, but locally and occasionally longer and more acute : edm : 1–2–3	Exploitation and shifting cultivation take marked toll of edaphic factors
2/16. HF : humid forest : as above, being converted to derived wooded savanna; relics numerous	Essentially as for 2 except for aerial changes caused by disturbance	Somewhat less humid, during drier periods	Similar to 2	Similar to 2	Exploitation and shifting cultivation take steady toll of edaphic factors
2/17. HF : humid forest : being converted to derived wooded savanna : relics rare to occasional	Temperature markedly greater due to removal of forest canopy	Sat. deficit greater due to removal of forest canopy : 4–7–9	Similar to 2 but less effective owing to edaphic changes caused by insolation	Similar to 2 but becoming more effective due to edaphic deterioration	Fuller exposure to insolation, cultivation inducing edaphic changes
2. A : HFS : humid forest subtropical (South Africa)	Mesotherm : 20–23° C and less	20–27, ranging to 13–20, sat. deficit 7–9+	900–1400 regular	Short-moderate, rarely severe, edm : 1–2–3	Some well conserved, others over exploited and converted to thicket grass and arable
3. HSFG : humid – sub-humid forest Guinean and Gabon subequatorial	Megatherm : +23° C	+27 to 20–27 rarely 15–20, sat. deficit 4–7–9	1400–2200 regular	Short, edm : 1–2–3	Extensive and severe
3/16. As above, being converted to derived wooded savanna, relics numerous	Essentially as for 3 excepting aerial changes cuased by disturbance	Somewhat less humid, during drier periods	Similar	Similar to 3 but becoming more effective due to edaphic deterioration	Steadily being converted to cultivation and pastoral (where tsetse permits)
3/17: Relics rare	Changes more marked than above	Changes more marked than above	Similar	More marked	More advanced conversion
4. HMF : montane forest (with variant 4A : HMSF humid-subhumid montane forest) equatorial and subequatorial	Mesotherm : due to elevation (1200–3500 m); 20–23° C, range moderate	20–27, rarely 15–20; and sat. deficit 4–7 rarely above	900–1400–1800, humid – subhumid variant 900–1400; regular, to occasionally irregular	Short-moderate very rarely severe, edm: 2–3 but in humid-subhumid variant : 4	Despite attempted conservation in some states, exploitation and shifting cultivation taking steady toll, with resulting deteriorating water resources
5. Freshwater swamp forest West Africa	Not discussed				
6. Mangrove equatorial/subequatorial	Not discussed				
GENERALIZED NORTH AND SOUTH OF EQUATOR, FOR BREVITY IN EXPOSITION					
7. SHWS : subhumid wooded savanna – variants 7A: more luxuriant north of equator 7B: less luxurant north of equator 7C: south of equator sub-tropical low, medium, upland, submontane elevations	Megatherm : +23; mega-mesotherm above 1000 m	20–27 during rains, but 13–20 during short dry periods; during longer dry seasons 13–20 to below 13; sat. deficit ranging from 7–9 to 13	990–1400–1800, regular to irregular	Moderate to fairly long and severe, edm 4–5 to 6	Extensive to local disturbance – due to shifting cultivation, and to pastoral over-stocking, where tsetse permits
Generalized : north and south of equator : not discussed					
7/8. Transition : SHWS/MSAWS subhumid/mild subarid wooded savanna, low, medium and upland elevations					Much as for 7 above
8. MSAWS : mild subarid wooded savanna, low, medium and upland elevations subequatorial	Megatherm : +23° C, mega-mesotherm above 1000 m	20–27 during rains, ranging to 13–20, sat. deficit ranging over 9–13	600–900–1100 less regular than in 7, irregular frequency	Fairly frequent dry spells often severe; edm 5–6	Extensive to local disturbance – erosion due to livestock: reduction locally of tsetse may intensify deterioration
8/9. MSAWS/SAWS transition subequatorial	Not discussed				Much as for 8 above
9. SAWS : subarid wooded savanna low, medium, upland elevations subequatorial	Megatherm : +23° C, mega-mesotherm above 1000 m	20–27 to 13–20, sat. deficit ranging 9–13–16	400–600, less regular than in 7, irregular frequently	Frequent dry spells, very severe, edm : 6–7	Extensive to local disturbance – erosion due to livestock
9/10. SAWS/AWS subarid wooded savanna, transition equatorial, subequatorial	Not discussed				Much as for 9
10. AWS : arid wooded savanna, equatorial, subequatorial	Megatherm, +23° C; mega-mesotherm above 1000 m	20–27 during rains, often 13–20 during dry periods; during long dry season sat. deficit 9–13–20	300–500, irregular, but in poorer rainy season down to 100 mm	Frequent dry/hot spells, very severe, edm : 7–8–9	Disturbance extensive to local, erosion due to over stocking
10/11. AWS/SD arid wooded savanna transitional to sub-desert wooded savanna, equatorial, sub-equatorial	Not discussed				Much as for 10
FOR BREVITY, ONLY SOME OF THESE REGIONS ARE VERY BRIEFLY SUMMARIZED					
Variants of sub-desert 11, 11/12A, 11/13, 12A 12B	Megatherm : 24–28° C; monthly maximum : 30–34				
11. Subdesert wooded savanna, (transitional to sahara) very arid subdesert	Monthly minimum : 23; (December/March)	Moister months (2-3): 13–20, rarely 20–27, edm: less than 13; saturation deficit : 13–20	(150–200–400)	edm 9–10–(11)	Highly variable : open short grass – wooded grassland, stunted thicket : locally to extensively and severely disturbed
12A. Subdesert/Karoo type (several faciations in aridity) including 12B the most arid	Megatherm/mesotherm 22–29° C; frost moderate/severe 40/90 days	Moister months 13–20; edm : less than 13; saturation deficit : 9–13	125–200–(300)	Marked, irregular and long; edm : 9–10–(11)	Locally and extensively and severely disturbed : overstocking, the cause of intense erosion
12A/14A. Example of grassland converted to Karoo; also noted in 14A : OGS – arid	Invasion of arid grassland by Karoo : Tidmarsh (1948), Acocks (1953). Noted invasion of grassland by Karoo species, mainly the non-palatable, lesser to wholly unacceptable browsing/grazing spp.				
Example of southern coastal desert : 13 : (Namib Desert) : D-SD-S (0–400–600 m)	Mean : 20–22° C. Mean maximum 27–29, mean minimum 11–15, absolute maximum 38+; frost in colder season on high ground	During medium moist months (2) : 13–20, 20–27; edm : 8–9; saturation deficit : 9–13 during edm's; benign influence of fogs	100–200–(350). Fogs blown inland by west and south west winds	edm : 9–10–11–(12); marked – but somewhat ameliorated by fogs	Local deterioration but efforts to control increasing
13. Main southern Saharan fringe – transition north Sahel and true Saharan desert	27–29° C; mean maximum 32–38° C, mean minimum 16–23; cooler during 2 months of Harmattan wind	During medium moist months (1)–2–(3); 13–20; during edm 2–4–7 saturation deficit 13–+20	Less than 50–200 to 350, July/September : 250–250	edm : 10–11–(12)	Ranging from nil to widely espaced to open desert : grassland, stunted wooded grassland to stunted open shrubland thicket; locally to more extensively despoiled, often severely
11 & 11/13. Somalia 'desert' : 'near desert' Phillips (1957)** : coast	27/29° C; coolest month 20° C	During 1–2 moister months 13–20–27, during edm : below 10 (coast effect); saturation deficit : 13–20–27	(25)–50–75–100	edm : 10–11; drought severe	Sub-desert/desert grassland and also with stunted shrubs and short trees severely despoiled, by livestock
Open grassland north and south of equator sub-equatorial but not sub-tropical South Africa	Not mapable at scale adopted; relatively small areas e.g. highland grassland in Kenya, Cameroon Mountain, Nigeria; doubtfully climax grassland Ethiopia (Montane)				Probably seral to thicket or short forest
A TENTATIVE GROSS CLASSIFICATION BIOCLIMATIC REGIONS : SOUTH AFRICA (PHILLIPS : 1959)					
OGS – ST : open grass savanna : subtropical South Africa : 14A: OGS – A : arid : also in 12A/14A in part	Mesotherm; mean minimum 4–8° C; frost severe, many weeks; monthly mean maximum December/February 18–23°	Less than 13–20, rarely 20–27; saturation deficit : 9–13	250–500	edm : 5–8, severe	Probably climax short open grassland; long continued overstocking has induced invasion of Karoo elements and stunted woody communities
14B. OGS – SA subarid	Mesotherm; somewhat milder than 14A	13–20; in moister months 20–27; saturation deficit : 7–9–13	500–750	edm : 3–8 fairly severe	Possibly climax widely where lower humidity and rainfall, prolonged and severe frost prevail; in more congenial sites *Acacia-Rhus-Maytenus* – other wood shrubs form short thickets; much overstocked
14C. OGS – MSA – SH mild subarid/subhumid	Mesotherm; cold, dry 'winter', frost moderate/severe	13–20–27; saturation deficit : 4–9	760–890	edm : 3–4–(5)	(i) In exposed high elevations – cold, frost, wind, the grassland probably climax (ii) Less exposed sites, woody elements occur in short thicket, if not killed by fire, probably grassland seral (iii) Congenial sites protected from fire, stunted forest relics remain; elsewhere grassland proclimax
14D. OGS – SH/H sub-humid/humid 3000–2000 m montane	Mesotherm; cool-cold; snow short periods annually at higher localities	20–27; saturation deficit : 4–7 below 4, in edm 7–9	900–1000+	edm : 1–3	Possibly climax *Themeda-Festuca* – other spp. grassland; fynbos; stunted evergreen thicket in sheltered sites; possibly climax locally; extensively disturbed severely
Generalized outline : M : 15 : arid, subarid, subhumid/(humid)					
Fynbos; macchia; AETFAT map 1981 : Cape shrubland 15A: arid : 15B: subarid 15C: SH/(H) : subhumid- 15D: humid	Mesotherm : October/March 17–21° C; April/September 10–14: frost nil to local, infrequent mild hotter in berg (hot, dry)	13–20 to 20–27; during drier periods less than 13–20; saturation deficit 4–7, to 9–13 in drier months lower, saturation deficit higher during berg winds	(300)–600–800 according to subregion; rain often follows berg winds	edm : 5–6 : arid 1–2–3: subarid 0–1 : sub-humid; drought severe in arid; moderate in subarid slight in subhumid	Extensively and severely disturbed : fire and poor pastoral control
15D: derived from destruction of humid forest and humid montane forest, Knysna type	Mesotherm, cooler, colder, notably in upland and montane localities	20–27–above 27; saturation deficit 4–7, but higher during berg winds	Former humid forest elevations 800–over 1000; former montane forest elevations 1000+ m	edm : 0. Drought : rare and moderate; edm : 0. Drought : rare and mild	Fynbos 60 years ago luxuriant today much despoiled, except where conserved and managed by state; efficient afforestation by state, exotics

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* edm : ecologically dry months, each with less than 25 mm rainfall

** In Int. Bank Report of Trust Territ. of Somaliland. Washington DC

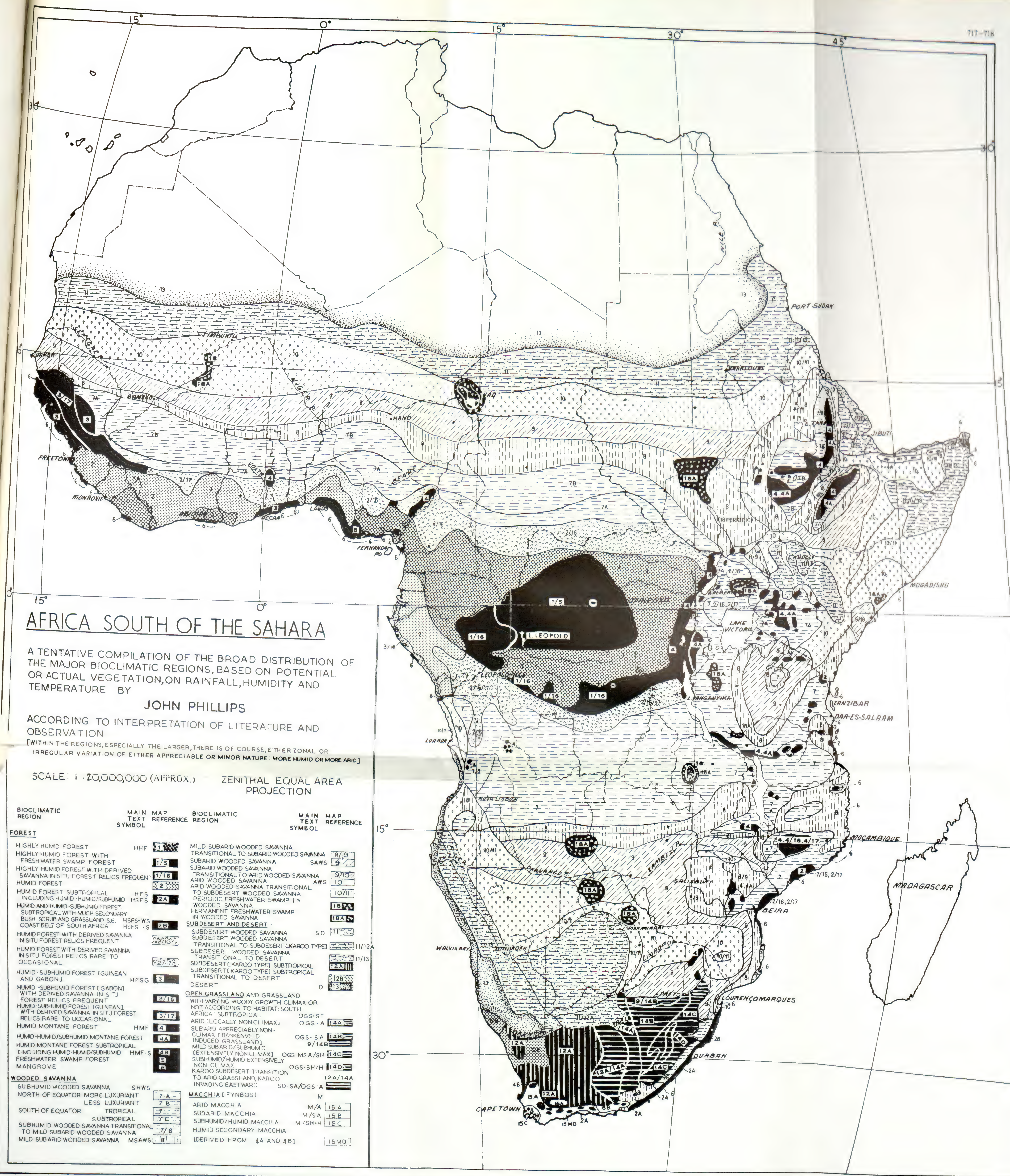
AFRICA SOUTH OF THE SAHARA
A TENTATIVE COMPILATION OF THE BROAD DISTRIBUTION OF THE MAJOR BIOCLIMATIC REGIONS, BASED ON POTENTIAL OR ACTUAL VEGETATION, ON RAINFALL, HUMIDITY AND TEMPERATURE BY
JOHN PHILLIPS
ACCORDING TO INTERPRETATION OF LITERATURE AND OBSERVATION
[WITHIN THE REGIONS, ESPECIALLY THE LARGER, THERE IS OF COURSE, EITHER ZONAL OR IRREGULAR VARIATION OF EITHER APPRECIABLE OR MINOR NATURE: MORE HUMID OR MORE ARID]
SCALE: 1 : 20,000,000 (APPROX.)
ZENITHAL EQUAL AREA PROJECTION
BIOCLIMATIC REGION
MAIN TEXT SYMBOL
MAP REFERENCE
FOREST
HIGHLY HUMID FOREST HHF 1
HIGHLY HUMID FOREST WITH FRESHWATER SWAMP FOREST 1/5
HIGHLY HUMID FOREST WITH DERIVED SAVANNA IN SITU FOREST RELICS FREQUENT 1/16
HUMID FOREST 2
HUMID FOREST SUBTROPICAL HFS
INCLUDING HUMID-HUMID/SUBHUMID HSFS 2A
HUMID AND HUMID-SUBHUMID FOREST: SUBTROPICAL WITH MUCH SECONDARY BUSH SCRUB AND GRASSLAND: S.E. COAST BELT OF SOUTH AFRICA HSFS-WS HSFS-S 2B
HUMID FOREST WITH DERIVED SAVANNA IN SITU FOREST RELICS FREQUENT 2/16
HUMID FOREST WITH DERIVED SAVANNA IN SITU FOREST RELICS RARE TO OCCASIONAL 2/17
HUMID-SUBHUMID FOREST [GUINEAN AND GABON] HFSG 3
HUMID-SUBHUMID FOREST [GABON] WITH DERIVED SAVANNA IN SITU FOREST RELICS FREQUENT 3/16
HUMID-SUBHUMID FOREST [GUINEAN] WITH DERIVED SAVANNA IN SITU FOREST RELICS RARE TO OCCASIONAL 3/17
HUMID MONTANE FOREST HMF 4
HUMID-HUMID/SUBHUMID MONTANE FOREST 4A
HUMID MONTANE FOREST SUBTROPICAL [INCLUDING HUMID-HUMID/SUBHUMID HMF-S 4B
FRESHWATER SWAMP FOREST 5
MANGROVE 6
WOODED SAVANNA
SUBHUMID WOODED SAVANNA SHWS
NORTH OF EQUATOR. MORE LUXURIANT 7 A
LESS LUXURIANT 7 B
SOUTH OF EQUATOR TROPICAL 7
SUBTROPICAL 7 C
SUBHUMID WOODED SAVANNA TRANSITIONAL TO MILD SUBARID WOODED SAVANNA 7/8
MILD SUBARID WOODED SAVANNA MSAWS 8
MILD SUBARID WOODED SAVANNA TRANSITIONAL TO SUBARID WOODED SAVANNA 8/9
SUBARID WOODED SAVANNA SAWS 9
SUBARID WOODED SAVANNA TRANSITIONAL TO ARID WOODED SAVANNA 9/10
ARID WOODED SAVANNA AWS 10
ARID WOODED SAVANNA TRANSITIONAL TO SUBDESERT WOODED SAVANNA 10/11
PERIODIC FRESHWATER SWAMP IN WOODED SAVANNA 18
PERMANENT FRESHWATER SWAMP IN WOODED SAVANNA 18A
SUBDESERT AND DESERT:-
SUBDESERT WOODED SAVANNA SD 11
SUBDESERT WOODED SAVANNA TRANSITIONAL TO SUBDESERT [KAROO TYPE] 11/12A
SUBDESERT WOODED SAVANNA TRANSITIONAL TO DESERT 11/13
SUBDESERT [KAROO TYPE] SUBTROPICAL 12A
SUBDESERT [KAROO TYPE] SUBTROPICAL TRANSITIONAL TO DESERT 12B
DESERT D 13
OPEN GRASSLAND AND GRASSLAND WITH VARYING WOODY GROWTH CLIMAX OR NOT, ACCORDING TO HABITAT: SOUTH AFRICA: SUBTROPICAL OGS-ST
ARID [LOCALLY NONCLIMAX] OGS-A 14A
SUBARID APPRECIABLY NON-CLIMAX [BANKENVELD INDUCED GRASSLAND] OGS-SA 14B
9/14B
MILD SUBARID/SUBHUMID [EXTENSIVELY NON-CLIMAX] OGS-MSA/SH 14C
SUBHUMID/HUMID EXTENSIVELY NON-CLIMAX OGS-SH/H 14D
KAROO SUBDESERT TRANSITION TO ARID GRASSLAND, KAROO INVADING EASTWARD SD-SA/OGS:A 12A/14A
MACCHIA [FYNBOS] M
ARID MACCHIA M/A 15 A
SUBARID MACCHIA M/SA 15 B
SUBHUMID/HUMID MACCHIA M/SH-H 15 C
HUMID SECONDARY MACCHIA [DERIVED FROM 4A AND 4B] 15MD
15°
0°
15°
30°
45°
30°
15°
0°
15°
30°
DAKAR
SENEGAL
TIMBUKTU
BAMAKO
FREETOWN
MONROVIA
ABIDJAN
ACCRA
VOLTA
LAGOS
NIGER
KANO
BENUE
CHAD
FERNANDO PO
KHARTOUM
NILE
PORT SUDAN
JIBUTI
MOGADISHU
STANLEYVILLE
L. LEOPOLD
LEOPOLDVILLE
LAKE VICTORIA
L. TANGANYIKA
ZANZIBAR
DAR-ES-SALAAM
LUANDA
NOVA LISBOA
WALVIS BAY
WINDHOEK
ZAMBEZI
SALISBURY
MOÇAMBIQUE
BEIRA
LIMPOPO
LOURENÇO MARQUES
DURBAN
CAPE TOWN
MADAGASCAR

Fig. 1.—Africa, south of the Sahara, showing the major bioclimatic regions.

succession; if not severely impeded by fire, shifting cultivation and the like, this kind of wooded savanna of former forest sites will develop into either advanced woodland or the earlier phases of forest.

Wooded savanna, not successional to forest

This community occurs in the form of Woodland, open woodland, wooded grassland, thicket, in habitats not ecologically conducive to the development of forest.

Space does not permit the detailed definition of these several growth forms of vegetation. Briefly, they are defined by their degree of stocking and espacement of stems of trees and large shrubs. None of these has either a true canopy or a true forest floor and soil as exists in a true forest.

Fynbos (Cape shrubland in AETFAT Map: 1982)

Fynbos is of local interest in several parts of montane East Africa, the Mediterranean, more extensively in the south-west districts of Cape Province and less so in the montane Eastern Cape Province. It is a sclerophyllous woody type of evergreen thicket bearing a rich flora, in places successional to Humid forest of Cape faciation, and now widely altered through pastoral and crop farming.

Karoo subdesert

This community comprises the South African forms of xerophytic and xeromorphic shrub, sub-shrub and succulent to sub-succulent vegetation, from about 0,3 m to 2 m tall, characteristic of portions of the more arid districts of Cape Province and beyond.

Desert of various faciations

These faciations occur in the Saharan fringe, Somalia, Ethiopia, portion of Kenya, the Namib and Angola: several instances of desert severity are given in the text (1959), and several types are merely noted in this note.

Grassland

Possible examples of climax grassland are noted in the text (Cameroun Mountain, Ethiopia, Namib), but several more extensive sectors of grassland in South Africa are considered, either successional or climax at varying elevations in South Africa and Lesotho (see Tabular Summary: AA, AB, AC, AD).

ROLE OF PHYSIOGRAPHY AND STUDY OF SOILS IN BIOCLIMATIC SURVEY

On a somewhat reduced but none-the-less still a fairly extensive scale in the Province of Natal, a number of African homelands in South Africa and in parts of Mozambique, I have been able to check the significance of examining and interpreting other parameters: physiography and pedological and other edaphic information. These, clearly, have cast light upon the admittedly somewhat broad information yielded by the bioclimatic unit. To some measure, the Loxton, Hunting survey (1974) teams in Mozambique derived the principles of taking into consideration the physiography (land form), slope, aspects, rainfall in the defining of natural units and their finer subdivision. This has been accomplished even more satisfactorily by the Soil and Irrigation Research Institute, in South Africa, in the defining of land forms (in press). These have certainly improved the sensitivity of the bioclimatic unit as a unit of physio-biotic comparison.

Physiographic and pedological criteria are illustrated for Natal in my maps and related references (Phillips, 1972), and the marked role of physiography is shown in Phillips (1973) for Lesotho.

THE OUTLOOK FOR BIOCLIMATIC STUDIES IN AFRICA

I ask that it be not held presumptuous that I should believe that the latest vegetation map of Africa (White, ed. 1983 UNESCO-AETFAT) holds the possibility of producing a far better bioclimatic map than ever I could have attempted. The application of Walter's climatic diagrams, especially derived for the investigation, could prove a useful undertaking: a map useful to students of developments within the whole biological field, could doubtless be completed within several years.

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A case for a vegetation survey in a developing country based on Zimbabwe

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ABSTRACT

The need for a vegetation survey in Zimbabwe, a developing country, is discussed. It is proposed that such a survey should produce a classification which is based on floristic criteria, and in which the vegetation types relate as nearly as possible to homogeneous environmental units. The practical application of such a classification is outlined with reference to the management of natural vegetation resources, land use planning and the preservation of species diversity.

RÉSUMÉ

ETUDE DE LA VÉGÉTATION DANS UN PAYS EN VOIE DE DÉVELOPPEMENT: LE CAS DU ZIMBABWE

Le besoin d'une étude de la végétation au Zimbabwe, pays en voie de développement, est discuté. Il est proposé qu'un tel relevé produise une classification basée sur des critères floristiques et dans lequel les types de végétation s'apparentent aussi étroitement que possible aux unités homogènes du milieu. L'application pratique d'une telle classification est tracée avec référence a la gestion des ressources végétales naturelles, programme d'utilisation des terres et la protection de la diversité des espèces.

REASONS FOR A VEGETATION SURVEY

Vegetation survey usually has the aim of accurately describing vegetation in terms of plant associations and of identifying relationship between the environment and these associations or their constituent species. In Zimbabwe, where large areas of land are still covered by natural vegetation, sound and objective classification of vegetation would have important practical application for both management and planning.

There are three main reasons that would justify a vegetation survey aimed at providing a classification system which has ecologically reliable and readily identifiable types. Such a survey (1) would help towards a more efficient utilization of natural vegetation; (2) could assist in land use planning; (3) is the only objective way available for selecting nature reserves.

1. *Vegetation survey in non-arable-land*

About two-thirds of the land in Zimbabwe is non-arable and land use is based on the utilization of the natural vegetation. In these areas, the vegetation constitutes the main natural resource and a vegetation survey which thoroughly describes, delimits and classifies existing plant associations on floristic criteria into vegetation types is of particular importance. It would provide a better basis than is presently available for research and advisory programmes and for management. Until such a framework exists, valid comparisons between vegetation of different areas and extrapolation of research results will remain difficult or unsound. A reliable classification of vegetation would, for instance, allow for a more objective selection of trial sites for the various research projects that are carried out to improve natural pastures; it would also make the resulting recommendations more specific.

Vegetation types are made up of individual species; each type has its characteristic species assemblage and within a type the species occur in more or less constant proportions. Once a classification of vegetation types is worked out and the total area that each type occupies is known, accurate assessments of the abundance of a species can be made. A vegetation classification based on floristic criteria is therefore the basis for all resource assessment studies. For instance, carrying capacity for livestock or game can be worked out more easily and accurately if the vegetation types of the grazing areas concerned are properly defined and described.

Non-arable lands also contain the most fragile ecosystems of the country. Mismanagement such as excessive removal of timber or over-grazing can easily cause irreversible changes like soil erosion or the loss of desirable plant species. It is imperative that these natural ecosystems are managed so that stability is maintained under utilization. The knowledge gained from a vegetation survey of the climax vegetation and the various successional stages that can occur is essential for assessing land potential, gauging degradation and planning management systems.

In rural areas the natural vegetation provides for many needs essential to the life of the people. Edible wild plants are an important constituent of the nutrient diversity in the people's diet. The traditional healers use the plants of the bush in their various remedies. Wild plants provide the raw material for much that is used in everyday life and more recently also for numerous homecraft industries. Enormous demands are made on the natural woodland to provide fuel for heating and cooking. Contrary to what may be expected from advances in modern standards of living, the reliance on the vegetation is likely to increase with increasing population

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pressure. To avoid habitat degradation, which is already far advanced in some areas, and also to prevent over-exploitation of useful plants, it is essential that utilization of the vegetation proceeds on a sustained yield basis. Vegetation survey will locate, assess and enable the monitoring of the indigenous vegetation resources and is therefore an important pre-requisite for their sound management.

2. *Vegetation survey as an aid in land use planning*

All prevailing environmental factors that significantly affect plant life are expressed in an integrated form by the natural vegetation. Vegetation types can therefore be used to indicate and identify land classes.

For agricultural planning and advice it is essential to have a classification of land types. Conventionally, land types are obtained by classifying land according to the physical characteristics of the environment that determines agricultural potential. The Agro-Ecological Survey by Vincent & Thomas (1960) is an example of this approach. It divides the country into climatic regions. These are further subdivided into natural areas primarily on soil characteristics but also on relief and sometimes minor climatic variations. A more refined version of the same approach is outlined by Whitlow (1980). Both are intended for general planning and assessing land potential on a country-wide scale. As a basis for detailed planning or a sophisticated advisory service, the categories made are too broad and in need of subdivision. What is required for this purpose is a classification in which the ultimate units correspond as nearly as possible to one type of environment. The land type survey carried out by N.C. MacVicar and his teams (MacVicar *et al.* 1974;1977) in South Africa aims at such a classification. In this survey areas with markedly uniform climate, terrain form and soil pattern are grouped into land types. Using all the important physical factors that affect plant growth, these land types are subdivided into units termed ecotopes which are areas with, for practical purposes, a uniform environment. There is a significant difference between one ecotope and any other.

In this country environmental units similar to the ecotopes described above are defined by the soil survey team of the Department of Research and Specialist Services. These units, for which ecotope is a convenient name, constitute the most refined land classes needed for practical agriculture. In areas where natural vegetation still exists each of these land classes or ecotopes is characterized by its own vegetation type and can therefore be identified and delimited by the vegetation that is supported by it.

It follows that where there is a reasonable cover of natural vegetation a vegetation survey can produce a similar classification of land classes to that achieved with a survey based on physical characteristics of the environment. This obviously does not mean that a vegetation survey can replace a soil survey in defining land classes since knowledge of the soil characteristics is essential. It does, however, mean that in relatively undisturbed areas a vegetation survey can greatly assist in recognizing and delimiting land classes. If a reliable vegetation classification is available before a soil survey is undertaken it can make the latter survey considerably easier. It is unfortunate that there is at present, despite extensive development, no vegetation team involved in land use planning.

3. *Vegetation survey to locate nature reserves*

Development in a country is often accompanied by large scale destruction of natural vegetation. As this spreads, plant species are endangered and it will become necessary to preserve species diversity. This can only be achieved successfully by protecting natural ecosystems in a nature reserve. It is important that the most suitable areas are chosen for nature reserves where maximum conservation can be achieved in the smallest possible area. Vegetation survey is essential for locating and selecting such areas.

The establishment of nature reserves is not just an emotional issue; they have a bearing on the survival of mankind and providing for them should be part of land use planning.

Most of what Man needs to sustain life comes from the plant kingdom. All cultivated plants have their origin in the wild. Advances in genetic technique mean that the circle of plant species that can be used for gene transfer in the breeding of a specific crop plant is widening. Distant relatives of crop plants are beginning to have value. The loss of even a single species means the loss of irreplaceable genetic material that has taken millions of years to evolve. Chemical compounds new to Man, some of which have important pharmaceutical or industrial use, are continually being discovered in wild plants. If plants are allowed to become extinct something might be lost that future discovery could otherwise have made valuable.

What is required initially, and has already commenced, is a vegetation survey of all national parks. Such a survey will reveal which plant species are already adequately protected. Surveys outside the parks will then indicate where further protection is necessary.

During development of the country, areas that are eminently suitable for nature reserves, and which the nation could afford to maintain as such, are denuded of their vegetation because their value as reserves is not recognized. This is another reason why it is important that a vegetation team is involved in land use planning.

PRESENT STATE OF VEGETATION SURVEY IN ZIMBABWE

The system of classifying vegetation currently used in Zimbabwe is essentially semi-physiognomic based on the growth form and appearance of vegetation (e.g. woodland, savanna, grassland), with the physiognomic 'types' further defined by apparent dominant species (Wild, 1965), Within 'types', e.g. *Brachystegia spiciformis/Julbernardia globiflora* woodland, there could occur large variations in species composition and quantity, and in environmental factors.

Existing classifications based on a subjective approach can be useful in country-wide mapping and approximate habitat descriptions but are not accurate enough for requirements in research, land management and land use planning as outlined above. Aware of these shortcomings, the National Herbarium has planned a vegetation survey which will satisfy these practical needs. To achieve this the following three points have been basic to the planning:

1. The vegetation classification obtained must be based on floristic criteria and each of the categories or 'types' produced must where possible correspond to one particular type of environment.

2. The need for a common approach to vegetation classification by all concerned with the management of natural vegetation has to be taken into account.

3. The methods used to sample and classify have to be objective so that results obtained by different people and in different places are comparable.

Although the eventual aim would be a classification which includes each type of vegetation found in Zimbabwe, initially one would work on areas where a vegetation survey has immediate benefits, thus gradually building up a complete coverage of the country. Once the natural vegetation units are delimited for a given area in a sound floristic classification, mapping of the types can take place on a scale consistent with the needs. However, even without a map the classification envisaged would allow anyone to recognize the different vegetation types merely by identifying the species that characterize each type.

Suitable sampling, measuring and analytical technique for a full-scale survey have been established in a pilot survey of woodlands around Salisbury (Robertson, 1979) and a survey of evergreen rainforest in the Eastern Districts of Zimbabwe. More recently these techniques have been applied, tested and perfected by the Department of National Parks and Wild Life Management in a vegetation survey of the Sengwa Research Area. Initial results are most encouraging and the same approach has now been adopted for vegetation classification in all major national parks.

To sum up: the need for a vegetation survey has become increasingly urgent and without it the following disadvantages will result:

1. Sound co-ordinated management of non-arable land and indigenous vegetation resources will be more difficult.

2. Accurate resource assessment of indigenous species will be impossible.

3. A valuable aid to land use planning will be made unavailable.

4. Adequate conservation of the species diversity cannot be achieved.

The costs involved for a national vegetation survey constitute a relatively small investment considering the long-term returns that would stem from it. The indigenous vegetation is diminishing rapidly; it is therefore important that a vegetation survey commences as soon as possible, especially since it is essential for a workable programme of flora conservation.

ACKNOWLEDGEMENT

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A survey of the coastal vegetation near Port Alfred, eastern Cape

R. A. LUBKE*

ABSTRACT

Detailed information on the colonization and succession of the sand dunes, dune slacks and rocky outcrops along the coast between the Riet and Kleinemonde Rivers is provided. The main reasons for the paucity of plants on the vast dune system are the movement of sand by wind and the inconsistent rainfall. Zonation of species along a dune transect is not particularly marked although a greater diversity of species is found in the dune slacks where an increased amount of seepage moisture occurs. Reclamation practices in blow-out areas have resulted in a pioneer cover of indigenous plants which should provide dense coastal scrub if the introduced *Acacia cyclops* is kept under control. Establishment of plants on the rocky promontories has occurred over a very long time and well developed communities and soils have formed. Salt spray and high winds are major controlling factors in the zonation of species along a gradient in this area.

RÉSUMÉ

UN RELEVÉ DE LA VÉGÉTATION CÔTIÈRE PRÈS DE PORT ALFRED, EST DE LA PROVINCE DU CAP

Une information détaillée sur la colonisation et la succession des dunes de sable, dépressions des dunes et affleurements rocheux le long de la côte entre les rivières Riet et Kleinemonde est donnée. Les principales raisons de la rareté des plantes sur le vaste système de dunes sont le mouvement du sable causé par le vent et les chutes de pluie irrégulières. La zonation des espèces le long d'un transect de dune n'est pas particulièrement marquée bien qu'une plus grande diversité d'espèces soit trouvée dans les dépressions des dunes où une quantité accrue d'humidité d'infiltration se produit. Des pratiques de restauration des sols dans les régions dégarnies par les vents ont résulté en une couverture pionnière de plantes indigènes qui devraient donner lieu à une formation côtière broussailleuse dense si on lutte contre l'envahissement de l'espèce introduite Acacia cyclops. *L'établissement de plantes sur les promontoires rocheux s'est produit au cours d'une très longue période et des formations végétales ainsi que des sols bien développés se sont formés. Les vents violents et la vaporisation de sel sont les principaux facteurs limitants dans la zonation des espèces le long de la côte dans cette région.*

INTRODUCTION

Apart from general descriptions of the coastal vegetation by Dyer (1937) and Comins (1962) very little has been written on the eastern Cape coastal vegetation. Unlike the coast of Natal and Zululand (Moll & White, 1978), the extensive dune systems along this coast are almost completely lacking in vegetation and do not show marked successional changes. The potential and real threat of these shifting dunes to surrounding farm and inhabitable land has lead to extensive reclamation programmes by the Department of Forestry (Keet, 1936; King, 1939; Walsh, 1968; Stehle, 1980).

It is important that more information on the extent and nature of the vegetation that becomes established naturally on the exposed dunes and rocky promontories is accumulated, before reclamation practices change the whole environment. This paper aims to provide some information about the vegetation along one section of the coast and explain the major role of the climate in modifying the environment. Changes in the soil and man-induced changes in the coastal ecosystem are also assessed.

The study area

The coastal strip between the Kleinemonde and Riet Rivers, about 12 km east of Port Alfred, is 4 km long and covers an area of approximately 350 ha. This portion of the 1820 Settler farm, Tharfield (Thorpe, 1972) bounded by the Port Alfred/East London road in the north and the sea in the south has been proclaimed a private nature reserve (Fig. 1).

The beach consists of about 100 ha of shifting sand dunes reaching approximately 50 m above sea level. The dune and dune slacks are sparsely vegetated in parts and the permanent vegetation begins with coastal scrub from 100 to 700 m from the shore. In protected areas the scrub becomes well established coastal forest with trees up to 10 m or more tall. In exposed areas the scrub has receded with the development of blow-outs (Oosting & Billings, 1942) which project often as far as 600 m into the scrub vegetation. In order to re-establish scrub in these blow-out areas the owner of the farm, Mr T. Webb, has followed the practice of the Department of Forestry of cutting bush clumps from other areas of the farm land used for grazing and using the cuttings to cover over the exposed sands (Fig. 2). This tends to stabilize the sand and provide a protective mulch for the germination and establishment of seedlings.

Parts of the shoreline are rocky with three striking promontories, called the Three Sisters, which project into the sea. These rocky buttresses vary slightly in size and form and rise up to 20 m from the wave-cut platform at sea level. Each has a steep cliff face on the seaward side, is flattened on top and then slopes towards the beach in the north (Fig. 3). Drift sands overlie the rocks on the beach side of the First and to a lesser extent to the Second Sister but the Third Sister in the east consists almost wholly of aeolianitic rock. This dune-rock is calcareous

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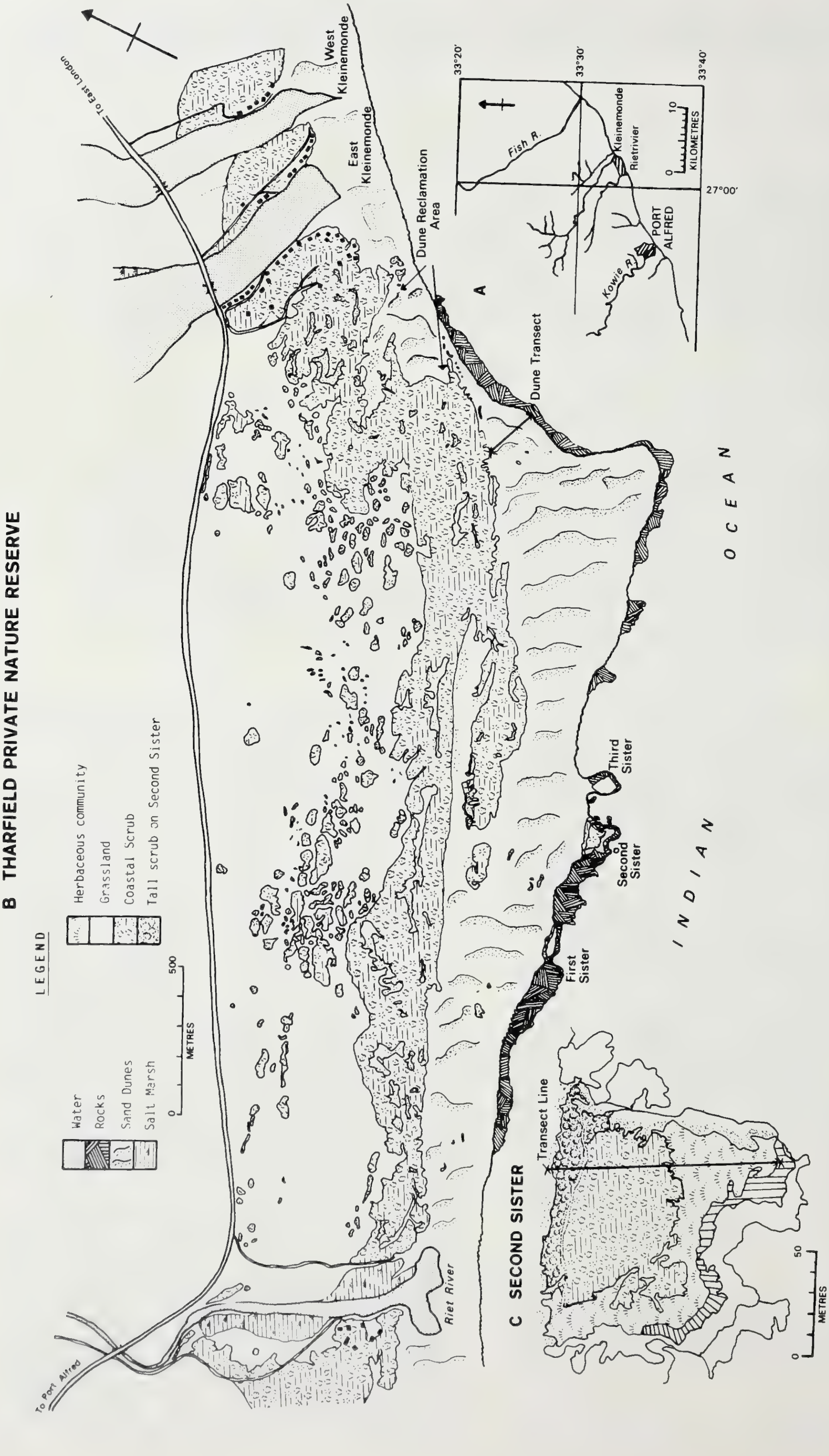

FIG 1.—The study area. A, Location of the Riet and Kleinemonde Rivers; B, Tharfield Private Nature Reserve as interpreted from air photos; C, A detailed map of the Second Sister.

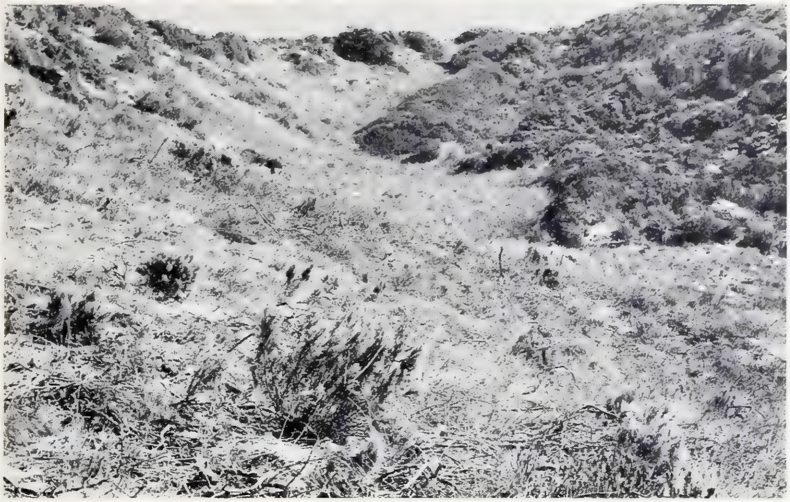

FIG 2.—Dune reclamation of a blow-out in the coastal scrub. Sand stabilizing plants are emerging through the bush cuttings which were placed over the dunes two years previously.

sandstone (Mountain, 1937) formed by lime cementation of ancient sand dunes, which on weathering forms variously shaped pinnacles, holes and small pockets. The dune-rock creates an attractive broken landscape along much of the coast east towards the Fish River and East London and west towards the Bushmans River and Woody Cape.

METHODS

Study sites were selected on the dunes and dune slacks (Fig. 1) wherever vegetation occurred. The foredunes studied were the only ones colonized along this stretch of coastline (Fig. 4). Fifty 1m^2 quadrats were randomly sampled on the foredunes and 68 in the dune slacks. The number of rooted shoots and percentage aerial cover of each species were recorded. A one metre wide belt transect was taken from the high water mark across the foredunes and dune slack up to the margin of the coastal scrub. (Fig. 5).

The reclamation area in the coastal scrub was divided into five regions on the basis of aspect and one m^2 quadrats were randomly sampled in each region, totalling 43 quadrats in all. The number of rooted shoots and percentage aerial cover of each species was recorded.

The rocky promontory chosen for study was the Second or middle Sister, because it showed a greater diversity of vegetation than the Third Sister and was more isolated from the dunes than the First Sister. Therefore the vegetation of this rocky promontory is not as disturbed and is more representative than that of the other two. A one m^2 belt transect was taken from the point first colonized by plants on the rocky cliff face to the dunes on the north side. An Abney level was used to measure the slope along the transect lines.

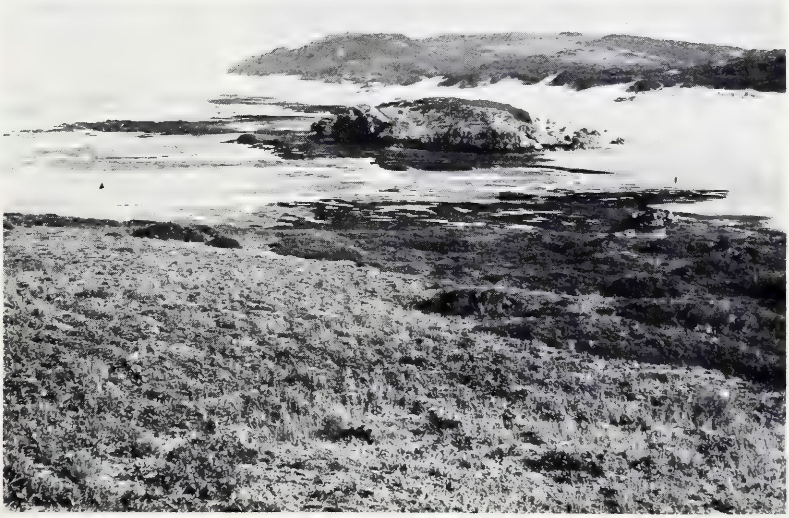

FIG 3.—View from the Second Sister looking west towards the First Sister. The herbaceous community is evident in the left foreground, grading into the low scrub community on the right.

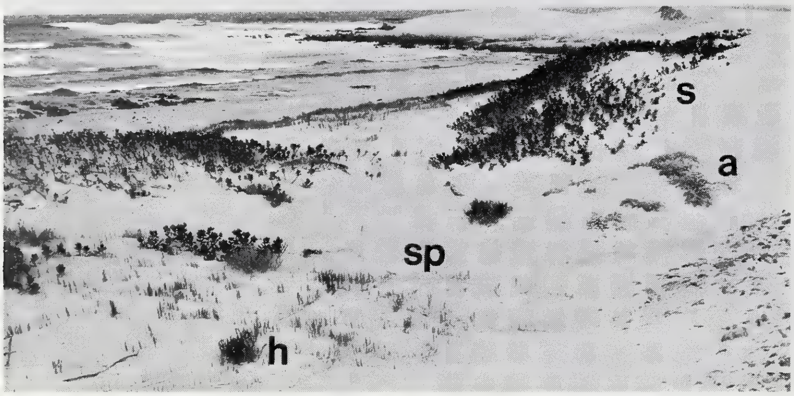

FIG 4.—The foredunes colonized by *Scaevola thunbergii* (sc), *Arctotheca populifolia* (a), *Sporobolus virginicus* (sp) and *Hebenstreitia cordata* (h).

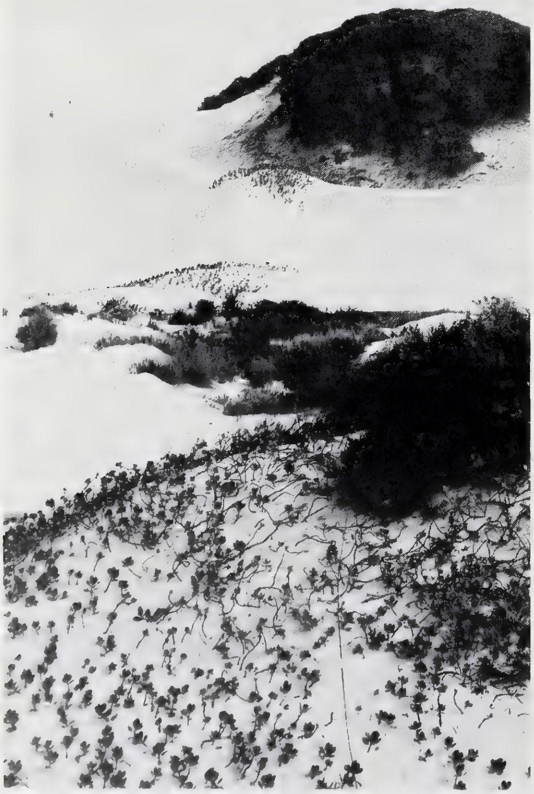

FIG 5.—Line of the belt transect taken through the foredunes up to the coastal scrub in the distance.

Soil samples were taken from the surface 10 cm of a number of random quadrats in the dune slacks and in the reclamation area. Similar samples were taken at intervals from the quadrats along the transects. The moisture content was determined for each sample by oven drying at 80–100°C. An estimate of organic content was obtained by combustion of oven dried soil in a muffle furnace at 400°C (Huntley & Birks, 1979). The pH was measured of each sample in water using a Metrohm pH meter and the conductivity of a 1 : 5 soil/water suspension was measured on an Electronic Switchgear conductivity meter.

RESULTS

The vegetation and floristic relationships.

Dyer (1937) gives a brief account of the species colonizing sand dunes and rocky cliffs in the Bathurst district. The general trend for both subtropical and Cape floristic elements to occur in the plant communities of the eastern Cape is also evident in this environment. *Scaevola thunbergii*, the abundant pioneer of tropical and subtropical foredunes occurs less frequently, its role being taken by other species such as *Arctotheca populifolia* or *Sporobolus virginicus* (Fig. 4), which are more frequent along the eastern Cape coast. *Myrica cordifolia*, *Metalasia muricata* and *Stoebe plumosa* are Cape species which very often supplant *Passerina rigida*, the dominant shrub colonizing the dunes behind the *Scaevola thunbergii* zone in Natal and Zululand (Moll & White, 1978; Ward, 1980).

Colonization of foredunes and dune slacks

The flora of the shifting sand dunes is poor and colonization of the extensive dune systems is sporadic. Where plants do occur they never cover areas of more than 50–100 m^2. Twenty species were recorded in the study area and the abundance of the 14 species which occurred in the quadrats sampled is given in Table 1. The distribution of species from the high water mark up to the coastal scrub is shown in Fig. 6.

Scaevola thunbergii is the primary colonizer of the fore dunes on the more sheltered eastern section of this coastline. *Sporobolus virginicus*, although occurring more frequently in the dune slacks, is abundant on the fore dunes as well (Fig. 4). In patches the introduced *Acacia cyclops* has become established as a low-growing creeping bush and may oust the indigenous vegetation even in this harsh

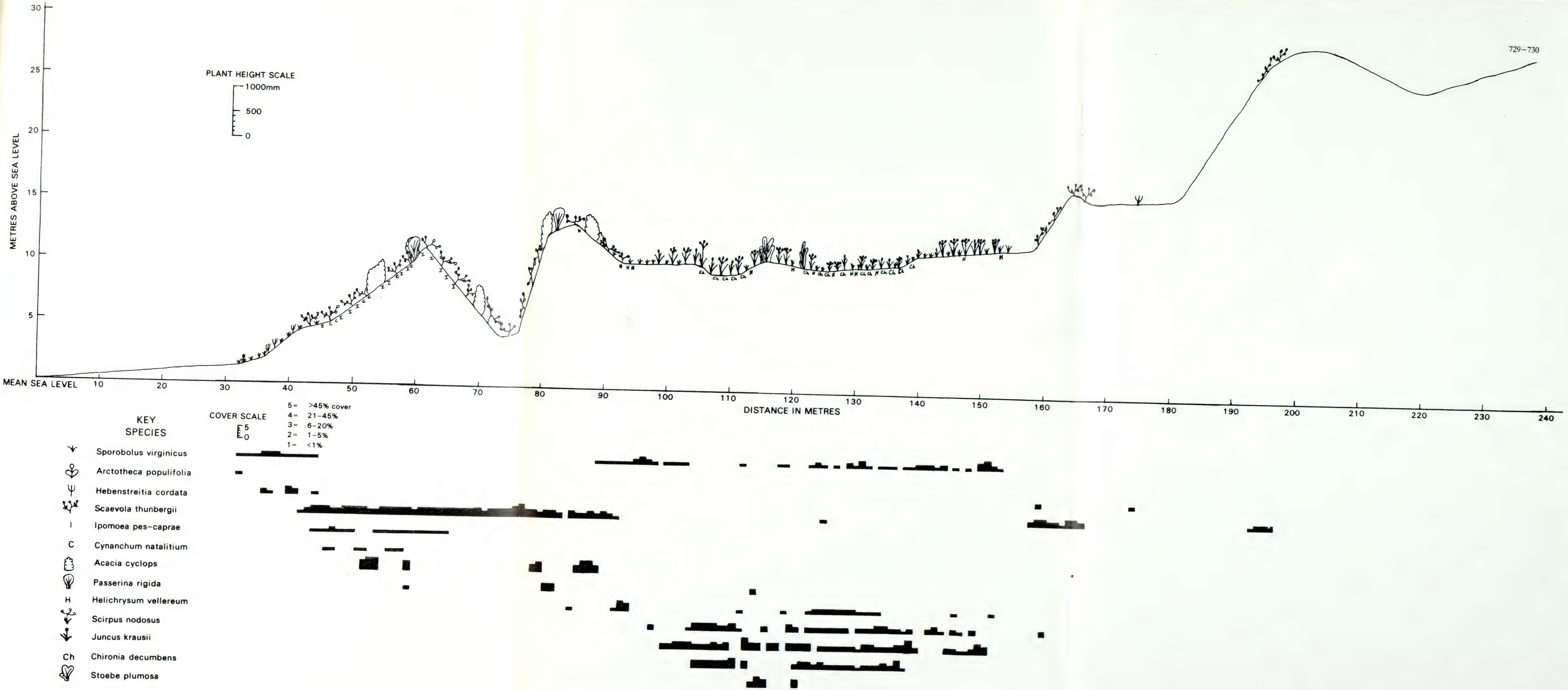

FIG 6.—Profile diagram of the vegetation on the dunes and dune slack near Kleinemonde. Species abundance is indicated in the lower part of the diagram as aerial cover in each 1m² quadrat along the transect.

TABLE 1. — Percentage frequency, aerial cover and density of species colonizing fore dunes and dune slacks

Species	% Frequency		% Aerial Cover		Density (plants m^{-2})	
	Dunes	Dune slacks	Dunes	Dune slacks	Dunes	Dune slacks
Exclusive to foredunes:						
Scaevola thunbergii	58	—	6,4	—	5,4	—
Acacia cyclops	2	—	1,8	—	0,02	—
Ipomoea brasiliensis	2	—	0,06	—	0,06	—
Tetragonia decumbens	2	—	0,2	—	0,2	—
Gladiolus gueinzii	2	—	0,01	—	0,02	—
Occurring in both habitats:						
Sporobolus virginicus	30	44,1	3,12	3,58	3,12	3,75
Arctotheca populifolia	8	22,05	1,0	1,23	0,62	1,04
Hebenstreitia cordata	6	1,47	0,44	0,01	1,01	0,11
Exclusive to dune slacks:						
Juncus kraussii	—	22,53	—	1,16	—	0,77
Scirpus nodosus	—	17,64	—	0,94	—	1,55
Helichrysum praecinctum	—	10,29	—	0,04	—	0,42
Chironia decumbens	—	7,35	—	0,51	—	0,52
Senecio elegans	—	1,47	—	0,01	—	0,01
Zalusianskya maritima	—	1,47	—	0,01	—	0,01

Additional species not recorded in quadrats: *Chrysanthemoides monilifera, Cynanchum natalitium, Mariscus congestus, Passerina rigida, Rhus crenata* and *Stoebe plumosa*.

environment. Although not abundant on the dune illustrated, in some areas *Ipomoea brasiliensis (=I. pes-caprae)* and *Arctotheca populifolia* become important pioneers, especially on the flattened dunes near estuaries.

In the dune slacks *Sporobolus virginicus* and *Arctotheca populifolia* are abundant in the drier areas and *Juncus kraussii* and *Scirpus nodosus* more frequent in wetter sand. Many more species appear in the dune slacks, often abundant in one particular dune slack but localized in extent. The transect (Fig. 6) traverses a rather moist luxuriant dune slack with many individuals and a greater diversity of species than most of the dune slacks that were sampled (Fig. 7).

Coastal scrub reclamation

The area in the coastal scrub which has been covered with brush to stabilize the sand occupies an area of about 7,9 ha. Of this area an estimated 5,2% has been colonized by *Acacia cyclops*. This *Acacia cyclops* thicket occurs in one region and was not sampled. The abundance of the species in the total area is indicated in Table 2. A total of 48 species were recorded, although 13 of these occur infrequently or in localized areas and were not recorded in quadrats. This is a large number of species to occur on unstabilized dunes and is due to the introduction of seeds of many coastal scrub species with the brush wood.

The protection and stabilizing effect offered by the branches (Fig. 2) allows for the germination of many species that normally would not occur on

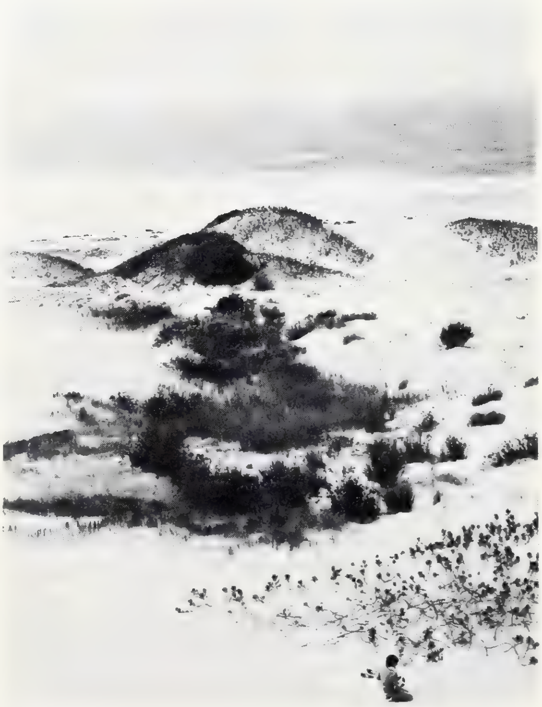

FIG 7.—Looking SE in the direction of the line transect. The moist dune slack in the centre of the photograph is dominated by *Juncus kraussii* and *Scirpus nodosus* with *Sporobolus virginicus* abundant in the drier areas.

TABLE 2. — Percentage frequency, aerial cover and density of species found in the reclamation area of the coastal scrub

Species	Frequency (%)	Density (Plants m^{-2})	Aerial Cover (%)
Ehrhata villosa	50,0	6,59	3,07
Helichrysum praecinctum	25,83	0,95	0,373
Senecio elegans	20,0	0,63	0,112
Senecio litorosus	17,5	0,45	0,051
Felicia echinata	14,17	0,25	0,244
Carpobrotus edulis	9,17	0,092	0,297
Ficinia aphylla	8,33	0,275	0,579
Stoebe plumosa	7,5	0,16	0,633
Polycarena cuneifolia	6,67	0,3	0,035
Brachylaena discolor	6,67	0,067	0,285
Zaluzianskya maritima	5,8	0,13	0,024
Rhus crenata	5,0	0,25	0,192
Passerina rigida	5,0	0,1	0,095
Helichrysum asperum	5,0	0,058	0,172
Pentaschistis heptamera	5,0	0,05	0,005
Anthospermum littoreum	4,17	0,075	0,493
Myrica cordifolia	4,17	0,05	0,243
Acacia cyclops	4,17	0,05	1,103
Eugenia capensis	2,5	0,05	0,005
Felicia capensis	2,5	0,05	0,005
Metalasia muricata	2,5	0,033	0,003
Acacia karroo	1,67	0,025	0,003
Rhoicissus digitata	1,67	0,017	0,083
Stipagrostis zeyheri var. *capensis*	1,67	0,017	0,068
Cynanchum natalitium	1,67	0,017	0,002
Kedrostis nana	0,83	0,017	0,083
Aloe sp.	0,83	0,0083	0,001
Berkheya heterophylla	0,83	0,0083	0,001
Clematis brachiata	0,83	0,0083	0,001
Knowltonia capensis	0,83	0,0083	0,001
Clutia daphnoides	0,83	0,0083	0,001
Helichrysum cymosum	0,83	0,0083	0,001
Heteroptilis suffruticosa	0,83	0,0083	0,001
Maytenus procumbens	0,83	0,0083	0,001
Salvia scabra	0,83	0,0083	0,001

Other species not found in quadrats: *Acacia saligna, Ammophila arenaria, Senecio pterophorus, Bulbine latifolia, Casuarina equisetifolia, Chironia baccifera, Chrysanthemoides monilifera, Dolichos falciformis, Hebenstreitia cordata, Helichrysum teretifolium; Ipomoea brasiliensis, Sarcostemma viminale and Scaevola thunbergii.*

exposed dunes. *Ehrharta villosa, Helichrysum* spp. and *Senecio elegans* were the species found most frequently in the reclamation area. The grass *Ehrharta villosa* becomes extremely abundant and well established in these conditions and although the aerial cover is low it has long rhizomes and plays a major role in dune stabilization. All of the abundant species are primarily secondary colonizers of blow-out areas in coastal scrub and are very different from the primary colonizers of fore dunes (Table 1).

Vegetation of the rocky promontories

The First Sister, that furthest to the west, consists of both herbaceous and low scrub communities, but it is similar in area and has been more disturbed than the Second Sister because it is more accessible to the beach. Of the 36 species recorded on the First Sister some, such as *Scaevola thunbergii* and *Senecio elegans*, are species of the sand dunes, and have not been found on the Second Sister. On the other hand, some of the 35 species of the Second Sister are shrubs not recorded on the First Sister. The Third Sister is much more exposed and consists almost solely of herbaceous plants, because very little sand has been deposited here. Only 16 species were recorded on this rocky buttress.

The Second Sister shows a distinct zonation of herbaceous and scrub communities (Figs. 1c & 3, Table 3). The profile diagram of the rocky promontory (Fig. 8) shows how the two community types are distributed and how the prevailing winds have affected the growth form of the plants. The dominant species of the herbaceous community are, in decreasing order of frequency: *Limonium scabrum, Plantago carnosa, Sporobolus virginicus, Delosperma littorale, Stenotaphrum secundatum, Aizoon rigidum* and *Gazania rigens* var. *uniflora*. The two grasses are also found in the scrub community although less common there. The dominant species in the scrub are *Maytenus procumbens, Rhoicissus digitata, Haemanthus albiflos* and *Eugenia capensis*. In areas closer to the sea or near to the land other species become locally dominant (Fig. 8).

There is a minimum of sand accumulation on the rocky cliffs and this lack of substrate and the strong winds prevents colonization by other species. Many of the species on the cliffs are halophytes also commonly found in estuaries, because there is an intense accumulation of spray on these rocks, especially during storms and high winds.

ENVIRONMENTAL FACTORS

The severity of the marine climate is the main limiting factor in the establishment of plants on both shifting dune sands and rocky promontories. The Cape is well known for its tempestuous conditions and unpredictable changes in weather.

Temperature

Extremes in temperature are common. In the summer, maximum air temperatures can exceed 40°C and in the winter the maximum temperature falls as low as 2–3°C (Schulze, 1980). Due to the high insolation and high air temperatures, the sandy and rocky substrates exhibit widely fluctuating temperatures. These soils with mainly physical components and low water holding capacity heat up to greater temperatures and fluctuate more markedly than soils with more organic matter and which dry out less rapidly. The soil temperatures may exceed 60°C in summer although this is only on the surface layers, because soil is a poor conductor of heat. At 20 cm depth the soil temperature was found to vary between 18,5–20°C on the dune reclamation site, whereas air temperature over the same 24 hour period in May, 1980 fluctuated from 18,5–29°C. Salisbury (1952) has also measured the moderating effect of depth in the soil on fluctuating temperatures in Britain. Soil temperatures over the 24 hour period were greatest on the fore dunes (22°C) followed by the dune reclamation site (20°C) and then the dune-slack (18°C). The dune-slack soil was also only subject to a 2°C temperature change over the 24 hour period compared with 6°C on the fore dunes. Plants in the sand dune environment must therefore contend with wide diurnal and seasonal fluctuations in temperature and variations in temperature at different depths in the soil.

Rainfall

The rainfall along this coast is rather eratic as Dyer (1937) has shown. The weather station at Great Fish Point, only a few km to the north east (33°32'S, 27°6'E) is situated just above the dunes at 73 m a.s.l. Over a 42 year period up to 1960, a mean average rainfall of 589,8 mm was recorded of which 60% fell in the summer months (Anon, 1965, Climate of South Africa). The annual rainfall chart shows a bimodal distribution with two maximum periods of March (mean 62,3 mm) and October (mean 69,0 mm) and the minimum rainfall in August (mean 32,1 mm).

Wind and sand movement

The effect of wind and sand movement is probably the major controlling factor in the distribution and establishment of plants in these coastal environments. The nearest weather station where wind records are kept is East London which experiences only about 11% calms in summer months and about 6% in winter months (Schulze, 1980). In the summer the predominant winds are easterlies or north-easterlies, but more intense winds occur in the winter months from the west or south-west. Therefore the sand dunes are orientated in a NW-SE direction and the greater movement of sand is from the west to the east. Blow-out areas in the coastal scrub face towards the beach in the direction from which the majority of prevailing winds arise (Fig. 1). The presence of vegetation on the dunes lowers the wind speed considerably, as does the profile of the dune itself, thus the wind speed in the slacks is considerably lower than on the dune face (Chapman, 1976).

Wind is also one of the major limiting factors in the establishment of vegetation on the cliffs and rocky promontories. The herbaceous plants on the exposed sides of the Three Sisters are able to become established by clinging to crevices and small pockets in the rocks where some sand may also accumulate. The pruning effect of the wind on the shrubs is apparent in the profile diagram across the Second Sister (Fig. 8). Due to increased transpiration and the chilling effect on the shoots and buds in exposed positions, growth is slowed down or stopped resulting in the pruned appearance of the shrubs.

Soil factors

The soil characteristics determined from soil samples taken from random quadrats in the dune slacks, the reclamation area, and along the line transects are listed in Table 4. The initial studies of the vegetation and soils of the different areas were made at different times in 1979 and 1980 but the soils were all re-sampled on 16th July, 1981 and re-analysed to give comparable results.

Soil factors are probably of secondary importance in the ability of plants to become established in coastal habitats, because a variety of dune species show a great range of tolerance to different soil conditions. Dunes usually have a neutral to alkaline pH which becomes more acidic with age (Ranwell, 1972). The pH of the dunes and dune slacks was between 8,00 and 8,2 (Table 4) whereas along the transect on the Second Sister where vegetation has been established for many years the pH drops

TABLE 3. — Percentage frequency of species on the Second Sister and the occurrence of all species on the rocky promontories

	Percentage Frequency on Second Sister			Occurrence on:	
Species (in order of occurrence from seaward side of Second Sister)	Herbaceous community	Scrub community	Total area	First Sister	Third Sister
Chenolea diffusa	23,73	0	11,67	+	+
Disphyma crassifolium	33,9	0	16,67	+	+
Aizoon rigidum	53,9	0	27,50	+	+
Limonium scabrum	94,92	0	46,67	+	+
Gazania rigens var. *uniflora*	62,71	0	30,83	+	+
Sporobolus virginicus	79,66	9,84	44,17	+	+
Plantago carnosa	79,66	0	39,17	+	-
Delosperma litorale	77,97	0	38,33	+	+
Falkia repens	15,25	0	7,5	-	-
Stenotaphrum secundatum	62,71	4,92	33,33	-	+
Mariscus congestus	8,47	11,48	10,00	-	-
Passerina rigida	5,08	9,84	7,5	+	+
Anthosperum littoreum	0	47,54	24,17	+	-
Carpobrotus edulis	0	31,15	15,83	+	+
Helichrysum teretifolium	0	16,39	8,33	+	+
Rhoicissus digitata	0	79,69	40,0	-	-
Euclea racemosa	0	32,79	16,67	+	-
Rhus crenata	0	9,84	5,0	+	-
Maytenus procumbens	0	83,61	42,5	+	-
Eugenia capensis	0	67,21	34,17	+	+
Haemanthus albiflos	0	68,85	35,0	+	+
Rhoiacarpos capensis	0	18,03	9,17	-	-
Cassine sphaerophylla	0	14,75	7,5	-	+
Rhus undulata	0	3,28	1,67	-	-
Euclea natalensis	0	1,64	0,83	-	-
Cynachum natalitium	0	9,84	5,0	+	-
Pavetta capensis	0	3,28	1,67	-	-
Secamone alpini	0	11,48	5,83	+	-
Sideroxylon inerme	0	6,56	3,33	+	+
Crassula nudicaulis var. *nudicaulis*	0	16,39	8,33	+	-
Chironia baccifera	0	6,56	3,33	-	-
Ficinia aphylla	0	3,28	1,67	+	-
Mimusops caffra	0	8,20	4,17	+	-
Chrysanthemoides monilifera	0	6,56	3,33	+	-
Maerua cafra			+	-	-
Solanum quadrangulare			-	-	+
Senecio elegans			-	+	-
Gladiolus guenzii			-	+	-
Scaevola thunbergii			-	+	-
Myrica cordifolia			-	+	-
Helichrysum argenteum			-	+	-
Senecio litorosus			-	+	-
Crassula expansa var. *filicaulis*			-	+	-
Scirpus nodosus			-	+	-
Lycium cf. L. campanulatum			-	+	-
Drosanthemum ambiguum			-	+	-
Acacia cyclops			-	+	-
Cassine maritima			-	+	-
Total number of species			35	36	16

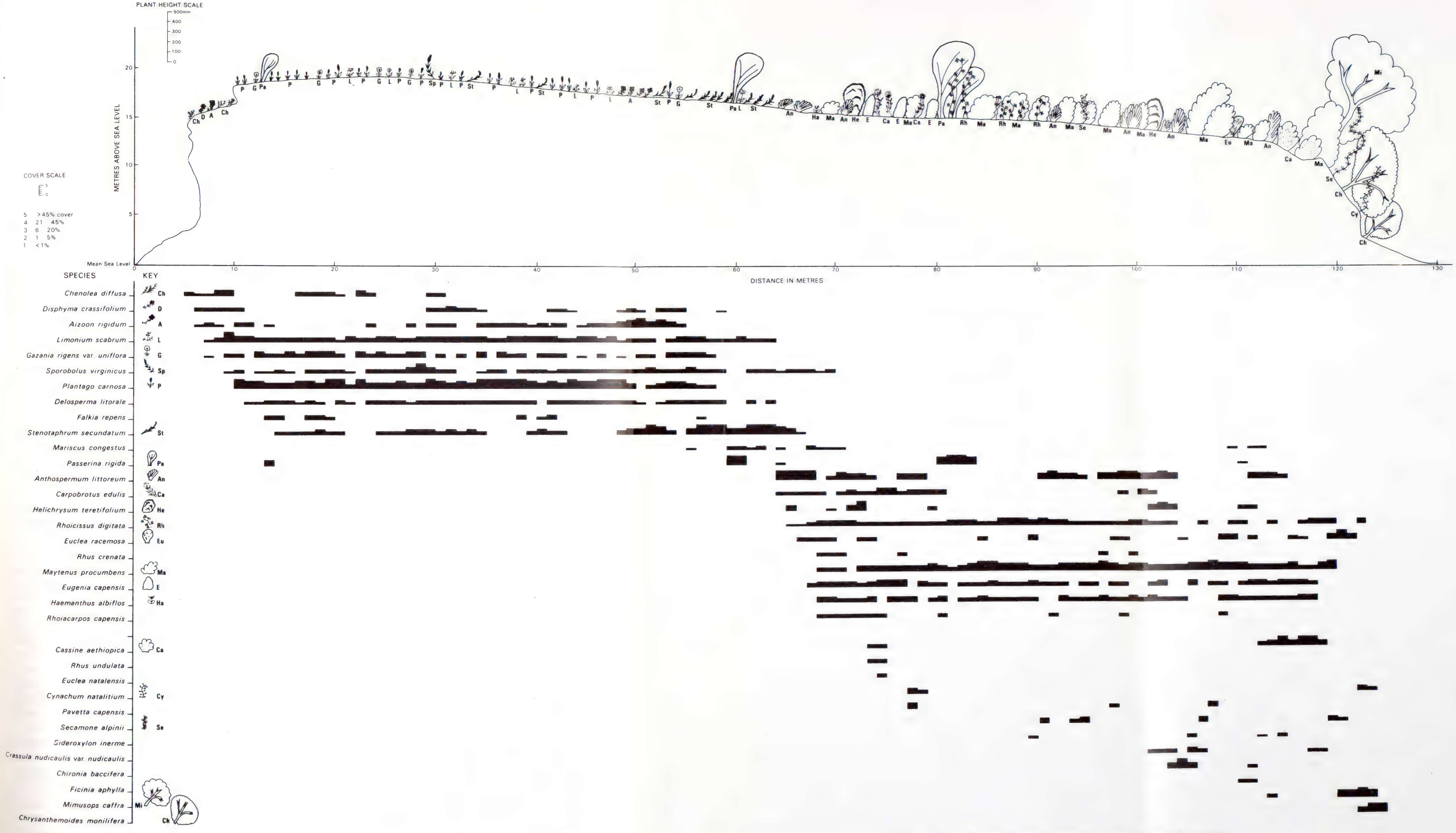

FIG 8.—Profile diagram of the vegetation across the Second Sister. Species abundance is indicated in the lower part of the diagram as aerial cover in each 1m² quadrat along the transect.

TABLE 4. — Characteristics of the soils (Mean ± std. error)

Locality	pH	Conductivity (millimhos cm^{-1})	Moisture content (%)	Estimated Organic content (%)
Fore dunes	8,02 (±0,01)	79,15 (±4,18)	1,64 (±0,30)	0,88 (±0,04)
Dune slacks	8,11 (±0,03)	120,54 (±14,16)	12,06 (±2,78)	0,675 (±0,045)
Dune Transect				
Zone I (Beach)*	8,1	290	2,21	1,36
Zone II (Fore dunes)	8,16 (±0,01)	72,76 (±6,02)	1,63 (±0,37)	1,08 (±0,09)
Zone III (Dune slacks)	8,16 (±0,02)	80,93 (±4,00)	11,66 (±4,57)	0,86 (±0,10)
Zone IV (Rear dune)	8,24 (±0,02)	68,05 (±4,72)	1,84 (±0,31)	0,74 (±0,08)
Coastal Scrub Reclamation Area	7,92 (±0,02)	64,53 (±1,40)	1,99 (±0,24)	0,99 (±0,05)
Second Sister				
Zone I (Rocky ledge)	8,20 (±0,20)	1600,0 (±770,0)	13,78 (±5,04)	4,42 (±2,66)
Zone II (Herbaceous exposed)	7,92 (±0,07)	435,0 (±118,57)	3,52 (±0,72)	2,13 (±0,51)
Zone III (Herbaceous)	7,83 (±0,12)	549,0 (±207,34)	9,78 (±2,05)	6,46 (±0,06)
Zone IV (Scrub)	7,96 (±0,05)	188,60 (±7,16)	7,81 (±0,64)	5,59 (±0,78)
Zone V (Tall Scrub)	7,78 (±0,13)	346,67 (±118,37)	5,88 (±2,50)	3,68 (±1,29)

* Not replicated

consistently. Likewise in the coastal scrub reclamation area the pH is slightly lower.

The base exchange capacity in sandy dune soils is low initially, but increases with the accumulation of organic matter. Salisbury (1925) found that the organic matter increased from below 1% to more than 5% after 200 years of vegetation establishment. The calcium carbonate content of these soils decreases correspondingly with age. The estimated organic content of the soils (Table 4) was not corrected for calcium carbonate and the values are probably exaggerated. However, on the young dunes the organic content is invariably less than 1%. On the Second Sister, however, organic matter has been accumulating over a long period and a more complex soil has developed. In the herbaceous community the 6,46% organic matter would represent an accumulation for more than 250 years on the basis of Salisbury's (1925) predictions.

On the mobile dunes accumulation of salts in the soils from sea spray may not be a problem because frequent flushing by rains will remove the salts from the sand. Although the actual salt content was not measured the conductivity gives an indication of salt accumulation in the soil. On the porous loose sands of the dunes the conductivity was generally less than 80 micromhos cm^{-1} but in the dune slacks a mean of 120,54 micromhos cm^{-1} was measured. On the beach (Zone I of the dune transect) and on the rocky ledges on the Second Sister, much higher conductivity readings were recorded. The effects of high tides and sea spray which inundates the rock cliffs is apparent and in the more well developed soil of the Second Sister consistently high readings were obtained because the soil could not be flushed of the salt ions as it is on the sand dunes.

The inconsistent rainfall and high porosity of sand which lacks a fine fraction results in a low availability of water for most of the year. The sand has a low water holding capacity and very low field moisture capacity of only about 7% (Salisbury, 1952). In the young dunes moisture content was generally less than 2%, except in the seepage areas of dune slacks where water accumulates close to the surface (Chapman, 1976), and was generally about 12% of the dry weight of the soil. The water table rises as the dune is built up (Hill & Hanley, 1914), and fluctuates with rainfall as has been reported from England (Willis *et al.*, 1959). On the rocky promontories the increased organic content gives better water retention and moisture content exceeded 10% in some zones of the Second Sister. There is a significant correlation between organic and moisture content of the soil ($r = 0,686$; prob $< 0,01$) in this area.

DISCUSSION

The absence of plants from these extensive dune systems can be explained by the migratory nature of the sand dunes due to persistent winds during most of the year. The movement of sand from the west to the east in winter and to a lesser extent in the reverse direction in summer, coupled with an inconsistent rainfall and high summer temperatures makes the establishment of plants on the dunes very sporadic, if at all.

The zonation of the plants along the transect can be explained in terms of the slight differences in soil conditions and climatic factors. The increased seepage of moisture, lack of spray and high insolation in the dune slacks allows for the establishment of a great diversity of plant species. Therefore, although no single factor can account for zonation on coastal dunes as has been reported by others (Oosting & Billings, 1942), the combination of environmental factors results in the zonation of species away from the shore. The importance of sea spray in controlling the distribution of species has been stressed (Oosting & Billings, 1942; Pammenter, pers. comm., 1979) and is currently been investigated for *Scirpus nodosus,* one of the dominant species of the dune slacks.

The re-establishment of plants in the reclamation area of the coastal scrub is being successfully achieved by covering the sands with brushwood. Although the microclimate and soil factors are changed only slightly by this action, the stabilization of the sand from further wind movement allows for regrowth of a great variety of coastal scrub and sand dune species. Since this study was carried out, the *Acacia cyclops* thickets have been removed and within the next 10 years a pioneer scrub community should be well established in this blow-out area.

The Three Sisters have well established plant communities which show various stages of plant succession. The high winds and spray are the major factors responsible for the distinct zonation of the plants in the area. The rocky ledge and very exposed herbaceous zones are generally characterized by *Chenolea diffusa,* a plant more common in salt marshes. The presence of halophytes indicates that salt spray is considerable in the region, a fact which is borne out from conductivity studies of the soil. With the accumulation of soil organic matter, which is indicative of the long period of establishment of plants on the rocky promontory, there is a correspondingly higher moisture content and substantial scrub communities have developed.

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Quelques exemples camerounais de liaison possible entre phénomènes géologiques et végétation

R. LETOUZEY*

RÉSUMÉ

Description morphologique, écologique et géographique des peuplements monophytiques (uniques en Afrique forestière humide) de *Gilbertiodendron dewevrei* (Caesalpiniaceae) dans le Sud-Est camerounais; caractère relictuel vraisemblable de ces peuplements; comparaison avec d'autres espèces grégaires parmi les Caesalpiniaceae et les Sapotaceae; hypothèse de l'abaissement de niveaux hydrostatiques.

Même hypothèse concernant les vallons forestiers encaissés du plateau soudano-zambézien de l'Adamaoua au Centre du Cameroun.

Etude d'un 'inselberg' gréseux, surplombant la forêt dense humide toujours verte du Sud-Ouest camerounais, avec végétation composite (de type 'miombo' mais comportant des plantes de littoral maritime ainsi que des éléments endémiques); hypothèse de mouvements épirogéniques récents, de mouvements tectoniques, de répercussions volcaniques (Mont Cameroun).

ABSTRACT

SOME CAMEROON EXAMPLES OF A POSSIBLE CONNECTION BETWEEN GEOLOGICAL PHENOMENA AND VEGETATION

The paper includes the following: a morphological, ecological and geographical description of the monophytic populations (unique in humid African forests) of Gilbertiodendron dewevrei *(Caesalpiniaceae) in south-east Cameroon; probable relic character of these populations; comparison with other gregarious species in the Caesalpiniaceae and Sapotaceae; hypothesis of the reduction of hydrostatic levels; — the same hypothesis related to the deep forested valleys of the Sudano-Zambezi plateau of Adamaoua in the centre of Cameroon and — a study of a sandstone 'inselberg,' overhanging the dense humid evergreen forest of south-west Cameroon, with compound vegetation (a type of 'miombo' but including maritime littoral plants as well as endemic elements); hypothesis of recent epirogenic movements, of tectonic movements, of volcanic effects (Mont Cameroun).*

La présente étude se propose d'attirer l'attention sur des facteurs pouvant contribuer à l'évolution de groupements végétaux; climats, sols et influences biotiques, topographie et hydrographie, voire paléoclimatologie — en elle-même, paraissent insuffisants pour expliquer parfois certaines situations actuelles. Trois exemples parmi d'autres possibles, camerounais ou africains, sont pris en considération.

1 LES FORÊTS À *GILBERTIODENDRON DEWEVREI*

Gilbertiodendron dewevrei (De Wild.) J. Léonard est une grande Caesalpiniaceae (35–45 m de hauteur, 3 (–5?) m de diamètre), à pivot assez développé au-dessous du plateau racinaire, à fût relativement court simplement évasé à la base, à écorce verdâtre-orangé-argenté se desquamant en grandes plaques, à cime compacte sempervirente (toujours avec quelques jeunes feuilles rouges pendantes); feuilles paripennées garnies de longues stipules aiguës caduques munies d'oreillettes, à limbe glanduleux sur la marge; fleurs, très odorantes, avec étendard bilobé lie de vin et 3 étamines fertiles; gousse aplatie, assez grande, ridée extérieurement, contenant 2–4 grosses graines.

Cette essence forme des peuplements pratiquement monophytiques (parfois 80% des grands arbres), avec arbres de tous âges, jeunes tiges, jeunes plants et semis, tous individus abondants et juxtaposés côte à côte, les strates moyennes et basses pauvres en éléments autres, les touffes herbacées et plantes rampantes très dispersées sur une dense litière de folioles, quelques grosses lianes diverses s'accrochant aux plus grands arbres.

Les taches de forêt, visibles sur photographies aériennes au 1: 50 000, sous forme d'un grisé 'moussu' caractéristique, atteignent souvent plusieurs hectares, parfois quelques dizaines d'hectares, exceptionnellement 1 000 et peut-être 3 000, voire 5 000 ha ± d'un seul tenant (Fig. 1). Ces taches se rencontrent dans le Sud-Est camerounais dépendant du bassin hydrographique zaïrois (ou au voisinage, par suite de phénomènes de capture reconnus), dans le Nord-Est gabonais, au Congo septentrional, dans le Sud-Ouest forestier du Centrafrique, enfin au Zaïre (surtout dans le Nord et le Nord-Est de la cuvette zaïroise), territoire où l'arbre (*limbali*) a autrefois été exploité sur une petite échelle, son bois étant de médiocre qualité. Hors de cet ensemble géographique, drainé par le fleuve Zaïre, *Gilbertiodendron dewevrei* se rencontre encore, beaucoup plus disséminé, dans la cuvette zaïroise jusqu'au Kwango et au Kasai septentrionaux; par pieds pratiquement isolés, il est connu en Angola (Nord Lunda) et — hors du bassin zaïrois — au Cabinda, dans le Sud-Ouest camerounais ainsi qu'en Nigeria (localement abondant dans la dépression de Benin). Dans ce territoire, l'arbre se localise, ce qui'il faut

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noter au passage, dans des forêts marécageuses et au bord de rivières, alors que partout ailleurs, les peuplements se trouvent en général dans des vallées mais sur sol sec, à l'abri des inondations permanentes ou temporaires qu'ils redoutent et hors de tous terrains marécageux; ils recherchent des sols sablonneux ou sablo-argileux de fonds de vallées mais — et c'est lá que le problème devient intéressant — les peuplements garnissent aussi, bien souvent, les flancs d'argile rouge latéritique de ces vallées et, à l'occasion, s'étendent, en continuité, sur les replats surplombants, à 10 m, 25 m, 50 m et plus parfois au-dessus du fond des vallées. L'extension possible des peuplements sur ces replats est entravée par la présence agricole humaine qui a contribué aussi et surtout à leur disparition; de même la forêt environnante, dont le caractère tant soit peu semi-caducifolié est manifeste, s'oppose à la difficile extension hors de la vallée, *Gilbertiodendron dewevrei* — avec sa graine lourde ayant tendance à rouler vers le bas des pentes — ne se régénérant bien et prolifiquement que sous son propre ombrage.

L'existence de ces peuplements 'suspendus' au-dessus des vallées est souvent passée inaperçue mais de multiples parcours dans le Sud-Est camerounais ont mis ce fait en nette évidence. Non moins notable est la présence, sur une colline forestière allongée barrant le confluent Sangha-Ngoko, de peuplements étroits, dans des vallons resserrés, vers 700 m d'altitude, alors que la plaine forestière environnante se situe vers 400–500 m.

Ces peuplements de *Gilbertiodendron dewevrei*, de vallées ou de replats, constituent des îlots de forêt toujours verte sous un climat en fait beaucoup plus propice à la forêt semi-caducifoliée, au Cameroun comme au Zaïre d'aprés les études de Gérard (1960). Ceci peut expliquer l'invasion assez rapide, favorisée parfois par des déprédations humaines, d'éléments de ce dernier type de forêt, souvent à semences anémochores ou zoochores, dans des trouées artificielles de peuplements de *Gilbertiodendron dewevrei* et même dans des trouées naturelles dues à la simple mort sur pied de très vieux arbres. On assiste ainsi, tant sur le terrain que sur photographies aériennes, à la dilution progressive et sans doute assez rapide, des peuplements envahis par la forêt environnante, lors même qu'il ne s'agisse de la destruction des peuplements du fait de l'homme.

Le caractère relictuel de ces peuplements de *Gilbertiodendron dewevrei* ne fait aucun doute et après les études préliminaires de Louis & Fouarge (1949) et de Devred (1958) sur cette espèce, Lebrun & Gilbert (1954) puis Gerard (1960) pour le Zaïre, enfin Letouzey (1968) pour une partie du Cameroun, ont pu formuler des hypothèses qui se trouvent incontestablement transformées en certitude à l'heure présente par nos observations camerounaises plus récentes.

L'existence de peuplements de replats au-dessus des vallées et l'évolution même naturelle de ces formations, atteste que la forêt à *Gilbertiodendron dewevrei* a occupé autrefois une place beaucoup plus importante en Afrique centrale et qu'elle est actuellement certainement en voie de disparition, au moins naturelle. L'action du climat actuel peut et doit être mise en cause certes, mais la disparition spontanée des peuplements de plateaux et de pente, voire de fonds de vallées, doit aussi être recherchée dans l'abaissement de nappes phréatiques dû lui-même à des variations des niveaux de base des cours d'eau, avec reprises d'érosion dans un passé certainement encore peu lointain; les vallées constituent donc des refuges, provisoires sans doute, de cette vieille forêt africaine.

Cette forêt à *Gilbertiodendron dewevrei* n'est d'ailleurs qu'un cas particulier, mais unique en son genre, de ces 'forêts á Caesalpiniaceae' qui, sous climat actuellement relativement humide, entourent

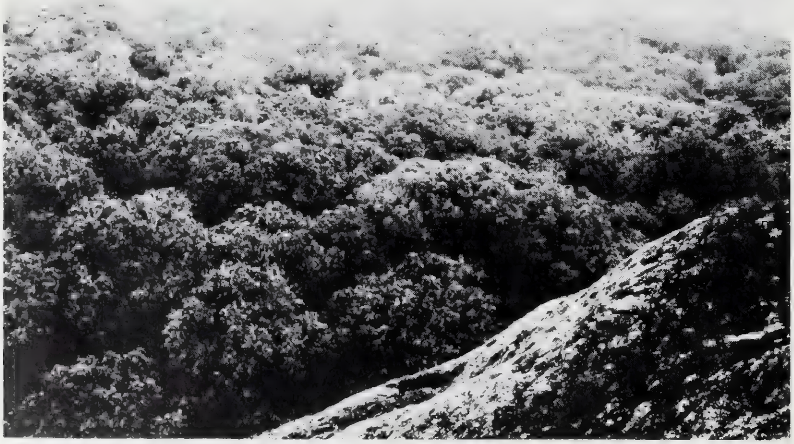

FIG. 1.—Cimes d'un peuplement de *Gilbertiodendron dewevrei.* Autour du rocher d'Ekok Edanbawa près Ngato, 100 km SW Yokadouma. Photo: R. Letouzey, 1973-03-29.

le Golfe de Guinée, en Liberia, en Côte d'Ivoire, en Nigeria, au Cameroun, au Gabon . . . Cependant, pour toutes les autres espèces de Caesalpiniaceae en cause, appartenant aux genres *Berlinia, Brachystegia, Cryptosepalum, Cynometra, Dialium, Didelotia, Hymenostegia, Julbernardia, Monopetalanthus, Oddoniodendron, Plagiosiphon, Tetraberlinia,* . . . les espèces concernées ne sont que grégaires et non sociales, à la différence du seul *Gilbertiodendron dewevrei* pratiquement. Pour ces espèces grégaires, des semis ou de jeunes plants ou des arbres plus âgés se rencontrent assez abondamment au voisinage des semenciers, mais englobés dans la forêt environnante; point ici de peuplements monophytiques et si l'on parle parfois de forêt à *Tetraberlinia tubmanniana* au Liberia, de forêt à *Cynometra ananta* en Côte d'Ivoire, de forêt à *Brachystegia mildbraedii,* à *Monopetalanthus pellegrinii* ou à *Tetraberlinia bifoliolata* au Cameroun, de forêt à *Monopetalanthus heitzii* au Gabon, de forêt à *Brachystegia laurentii* au Zaïre, ces formations, quant à leur structure, sont beaucoup moins caractérisées que les forêts à *Gilbertiodendron dewevrei* du bassin zaïrois d'Afrique centrale.

Les Caesalpiniaceae représentent un élément floristique fondamental des actuelles forêts denses humides toujours vertes de l'Afrique occidentale et centrale; au Cameroun même, cette famille groupe quelque 60 genres représentant seulement 150 espèces et le genre *Gilbertiodendron* quant à lui (voisin mais différent du genre américain *Macrolobium)* rassemble une quinzaine d'espèces camerouno-gabonaises, ainsi qu'une vingtaine d'espèces autres, aucune de ces espèces n'étant sociale, tout au plus grégaires, si l'on fait abstraction de minuscules peuplements formés çà et là par certaines d'entre elles, telle *Gilbertiodendron brachystegioides* au Cameroun (Letouzey & Mouranche, 1952). Parmi les deux autres familles de Légumineuses, en ce qui concerne les arbres constituants essentiels de forêts, aucun fait analogue de sociabilité ne se rencontre et on peut au plus mentionner au passage quelques espèces ± grégaires, telles *Calpocalyx heitzii* ou divers *Newtonia* parmi les Mimosaceae.

Le problème est encore plus inconsistant pour d'autres familles, toujours en ce qui concerne les arbres constituants des forêts denses humides. Si des espèces héliophiles, à semences anémochores bien souvent, envahissent massivement des clairières naturelles ou artificielles, telles *Terminalia superba, Triplochiton scleroxylon, Lophira alata, Desbordesia glaucescens* et d'autres, telle encore *Aucoumea klaineana* au Gabon, l'avenir des peuplements temporaires qu'elles forment est éphémère et elles se diluent très rapidement dans la forêt environnante où leur régénération y est totalement entravée. Quelques Sapotaceae grégaires, à tempérament sciaphile, à semences barochores, appartenant au genre *Lecomtedoxa* en particulier, seraient à rapprocher des Caesalpiniaceae.

Un cas cependant fort troublant en matière de paléophytogéographie a déjà été signalé dans le Sud-Est du Cameroun (Letouzey, 1978): Au sommet d'une petite colline forestière, rassemblés sur moins de 2 hectares seulement et mélangés à d'autres espèces arborescentes, 7 genres de Sapotaceae groupant 11 espèces, dont 2 très abondantes, 6 abondantes et 3 plus dispersées, ces espèces étant représentées par des arbres de bonnes dimensions, avec régénération très sporadique; cette tache de forêt — où les Sapotaceae occupent une place si particulière — est de type primaire, avec arbres morts sur pied, peu de lianes, sous-bois dégagé, et se situe au sein d'une région couverte d'une forêt à tendance semi-caducifoliée; climat, terrain, influences biotiques ne paraissent guère en mesure d'expliquer cette curieuse aberration phytogéographique; le fait peut cependant être rapproché d'une autre anomalie: Dans deux gorges rocheuses situées dans un massif montagneux de l'Ouest-Cameroun, entre 1 500 et 1 800 mètres d'altitude, se rencontrent des vestiges de typique forêt submontagnarde, ici encore truffée par une quantité relativement importante de Sapotaceae, avec 5 genres et 5 espèces, 3 représentées par un grand nombre de tiges, les 2 autres de moindre abondance; la topographie peut ici expliquer la prolifération d'espèces sciaphiles à graines lourdes, mais non l'existence même de ce rassemblement d'espèces. Pour qui connaît le comportement normal de la famille des Sapotaceae en forêt dense humide africaine, on ne peut s'empêcher, à nouveau, de faire appel au caractère relictuel de tels groupements, sous l'influence de causes autres que les causes écologiques évoquées habituellement pour expliquer la présence de tel ou tel groupement. Il est ici encore bien tôt pour avancer quelques hypothèses, vraisemblablement ressortiraient-elles encore de ces variations de niveaux hydrostatiques mentionnées à propos de *Gilbertiodendron dewevrei.*

2 LES VALLONS FORESTIERS ENCAISSÉS DU SECTEUR SOUDANO-GUINÉEN

Au Cameroun, ce secteur est essentiellement représenté par le plateau central de l'Adamaoua, château d'eaux en toutes directions, situé vers 1 000–1 200 m d'altitude, couvert de pâturages — fréquemment surchargés — sur de vastes surfaces et de savanes à Andropogoneae, ravagés par les feux de saison sèche et parfois cultivés en manioc, et constellés de petits arbres et d'arbustes pyrophiles (essentiellement *Daniellia oliveri* et *Lophira lanceolata* dont la prolifération est semble-t-il en grande partie d'origine anthropique); ce plateau est entaillé de vallons où alternent forêts (de type forêt dense humide semi-caducifoliée à tendance xérique) et terrains cultivés, surtout en maïs, ces derniers bien souvent établis au détriment et par destruction des premières.

En fait, tant pour la flore soudano-zambézienne des savanes que pour la flore guinéo-congolaise des vallons forestiers, on constate sur le plateau, allongé sur quelque 600 km en longitude et large de 100 à 200 km en latitude, quelques différences floristiques entre les parties occidentale et orientale. Incontestablement le climat est relativement moins humide et plus continental à l'Est qu'à l'Ouest, mais les modelés du terrain sont aussi un peu différents. Le socle du plateau, de granites et de migmatites, traversé par des failles WSW-ENE, est surmonté de pointements et revêtements volcaniques tertiaires et quaternaires au Centre et surtout à l'Ouest où les reliefs atteignent 2 500 m. Le plateau lui-même, qui seul retient ici l'attention, supporte des sols ferrallitiques rouges, accompagnés de lithosols vers l'Ouest accidenté et de zones cuirassées, particulièrement développées dans l'Est pénéplané. Dans cette zone orientale, de véritables cirques d'effondrement anciens, d'apparence fossilisés, profonds de dix à vingt mètres, ferment les vallons vers l'amont; ces accidents, de type lavakes malgaches, sont beaucoup plus rares vers l'Ouest.

Or il est encore possible de trouver, fort rarement il est vrai, sur le rebord de l'effondrement ou au voisinage immédiat, quelques grands arbres et îlots en nette voie de disparition, de la même forêt que celle occupant le fond des vallons; ces grands arbres appartiennent à des espèces très caractéristiques *(Aubrevillea kerstingii* (Fig. 2), *Eriocoelum kerstingii, Maranthes kerstingii, Beilschmiedia anacardioides, Erythrophleum suaveolens, Khaya grandifoliola, Vitex cienkowskii, . . .),* de même les strates arborescentes inférieures, arbustives, herbacées et lianescentes (Letouzey, 1968). Ces éléments relictuels, surplombant les vallons, sont-ils les vestiges de l'ancienne forêt de l'Adamaoua?

Pour divers auteurs (Aubréville, 1948), la végétation primitive aurait été constituée par des forêts denses sèches assez analogues aux forêts zambéziennes actuelles. Les témoins ci-dessus viendraient peut-être à l'encontre de cette théorie, surtout depuis la découverte (Letouzey, 1969) de vestiges forestiers et même d'un îlot de forêt assez étendu (en voie d'intense destruction pour cultures de maïs cependant), dans l'Ouest de l'Adamaoua vers Banyo; ici se retrouvent les mêmes constituants que ci-dessus, mais les espèces arborescentes y prennent des ports de grands arbres de savane, les strates basses et herbacées demeurant de type analogue à celui des forêts semi-caducifoliées; on rejoint ainsi l'hypothèse de Keay (1959).

Les effondrements de vallons correspondent incontestablement à des reprises de cycles d'érosion par suite de variations de niveaux de base de cours d'eau et l'on se retrouve devant des faits analogues à ceux évoqués à propos de *Gilbertiodendron dewevrei;* la transformation physionomique en grands arbustes de savane est aussi en liaison semble-t-il avec de tels facteurs (de même la perte des racines échasses de *Uapaca togoensis* constatée vers Banyo). Depuis quelques siècles s'ajoutent les incursions agricoles et pastorales de l'homme ainsi que les feux pour certainement accélérer la disparition de la forêt semi-caducifoliée à tendance xérique du plateau; la cause lointaine des variations de niveau topographique peut être recherchée dans le jeu de failles tectoniques importantes et de phénomènes volcaniques, connus comme relativement récents, ce qui conduit au dernier volet de ce tryptique camerounais.

3 L'ÎLOT TÉMOIN DE NKOLTSIA

Décelé sur photographies aériennes et rapidement prospecté par nous en janvier 1974, ce site fort original a fait l'objet d'un travail botanique particulier (Villiers, 1981) tant son intérêt est certain.

La colline en cause (Nkoltsia) constitue un château-fort rocheux, dressé au milieu et au-dessus de la forêt dense humide à Caesalpiniaceae environnante, avec des falaises verticales de 50 m de hauteur et plus, cette colline étant située à 35 km seulement de la côte océane (non loin d'ailleurs de Bipindi, à moins de 20 km de là, où séjourna G. Zenker pendant 25 ans, sans en connaître semble-t-il l'existence); l'altitude atteint ici 488 m, alors que la plaine environnante se situe vers 100 m, le dessus de la colline formant une vaste dalle un peu inclinée d'une cinquantaine d'hectares. La roche paraît être un grés détritique non sédimentaire, quoique certains géologues signalent cette colline comme quartzitique; des failles importantes la traverse et

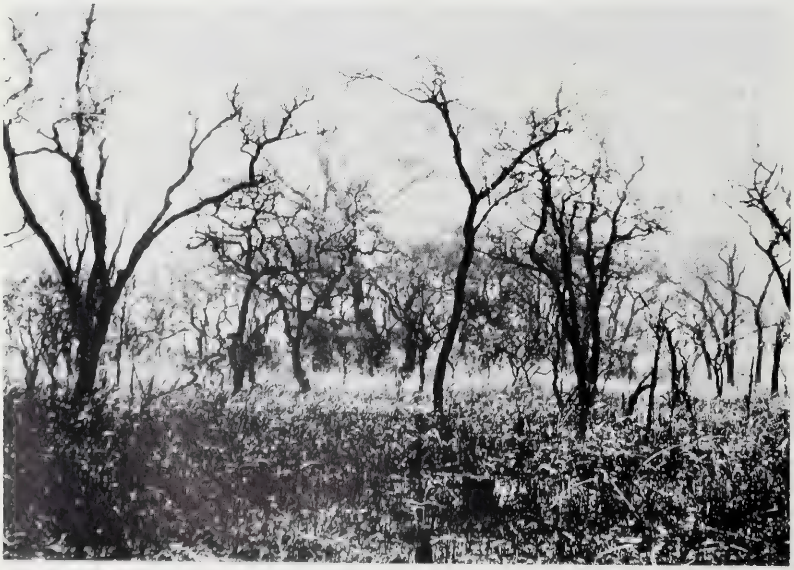

Fig. 2.—Bosquet avec grand *Aubrevillea kerstingii,* en savane boisée à *Terminalia glaucescens,* dominant un vallon forestier encaissé. Mbamkim-Djaoro Ndo, 10 km ESE Tibati. Photo: R. Letouzey, 1959-12-08.

depuis fort longtemps elle semble être à l'abri des incursions et déprédations humaines.

L'originalité de cette dalle provient du fait qu'elle supporte d'une part une forêt basse claire à *Julbernardia letouzeyi* (Fig. 3), avec arbustes et petits arbres tortueux, clairiérée par endroits, forêt que l'on rattache aisément aux forêts zambéziennes australes, particulièrement à l'ordre *Xerobrachystegion* de Schmitz (1950) et d'autre part des prairies à euphorbes cactiformes (*Euphorbia letestui,* Fig 4), Mais l'originalité (que l'on pourrait considérer comme un témoignage paléoclimatologique) ne s'arrête pas là car, constituants aussi de la forêt basse claire (certains vivant également dans les prairies à euphorbes cactiformes) se trouvent également rassemblés ici des éléments faisant normalement partie de la végétation des cordons littoraux sablonneux, en particulier *Syzygium guineense* var. *littorale* et *Manilkara obovata,* auxquels on peut ajouter des arbustes et plantes de ces cordons, de zone d'arrière-mangrove ou de zone forestière littorale, de là plus rarement à l'intérieur des terres; la liste de ces espèces littorales secondaires est assez importante, avec: *Afzelia bella* var. *bella, Baphia nitida, Bertiera subsessilis, Cassipourea barteri, Leptactina mannii, Psorospermum tenuifolium, Costus lateriflorus* et même *Angraecum eichleranum,* sans doute aussi *Eugenia afzelii* (ou *E. whytei?*), pour qu'il soit difficile d'admettre que le rassemblement de cette dizaine d'espèces puisse s'expliquer par des transports aviaires.

Dernier élément d'originalité de cette colline, et non des moindres, la présence d'endémiques, soit au sens strict du terme (ainsi *Amphiblemma letouzeyi, Calvoa calliantha, Julbernardia letouzeyi),* soit d'espèces fort rares, très localisées çà et là au Cameroun ou ailleurs (*Begonia jussiaecarpa; Costus lateriflorus* et *Euphorbia letestui* (aussi au Gabon);

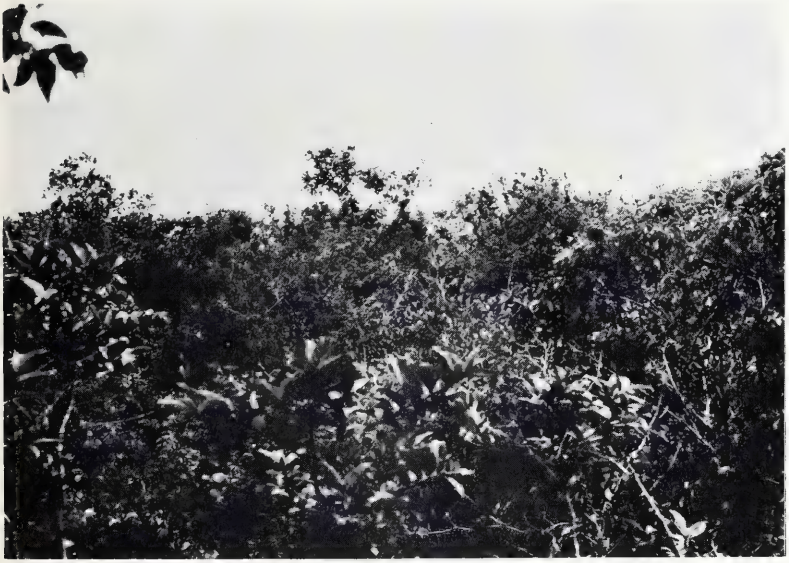

FIG. 3.—Forêt basse claire à *Julbernardia letouzeyi.* Colline Nkoltsia, 50 km NE Kribi. Photo: R. Letouzey, 1974-01-12.

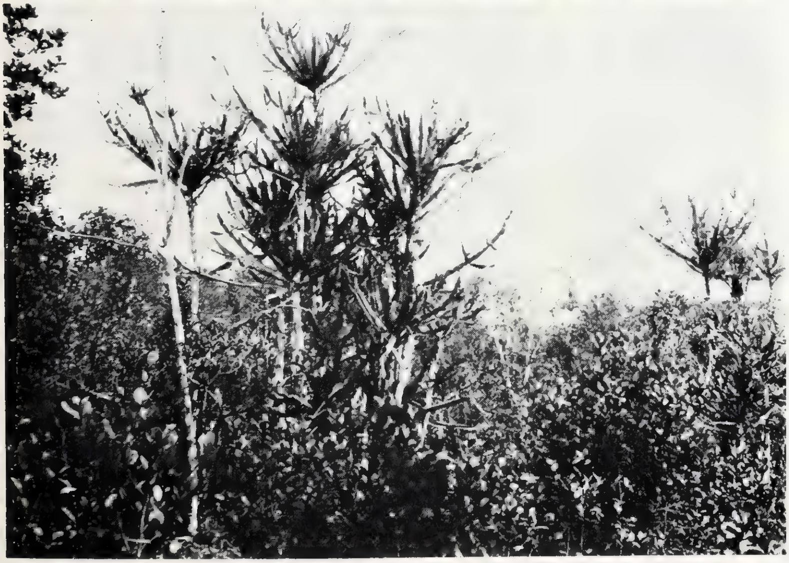

FIG. 4.—Prairie à *Euphorbia letestui.* Colline Nkoltsia, 50 km NE Kribi. Photo: R. Letouzey, 1974-01-12.

Bulbophyllum fuscoides (aussi à Fernando Po); *Genyorchis platybulbon; Polystachya victoriae; Mesanthemum jaegeri* (aussi en Sierra Leone et en Nigeria); *Dissotis rupicola* d'Angola), soit encore vraisemblablement parmi quelques plantes non à ce jour identifiées *(Dracaena* sp., *Gladiolus* sp., *Homalium* sp., *Panicum* sp., *Phyllanthus* sp., *Psychotria* sp., *Rutidea* sp.), ou parmi des mousses et hépatiques restées aussi indéterminées. L'étude de Villiers a porté également sur ces bryophytes et là aussi peuvent être relevés quelques faits curieux: une mousse *(Fissidens purpureo-caulis)* et deux hépatiques *(Calypogeia fusca* et *Frullania apicalis* var. *camerunensis),* espèces normalement d'altitude, retrouvées ici à 400 mètres (à mettre en parallélisme la présence de *Podocarpus latifolius* — incl. *P. milanjianus* — connu à basse altitude au Cameroun et au Congo.)

La présence de reliques zambéziennes et surtout d'espèces littorales, accessoirement d'endémiques, dans un site entouré d'une forêt dense humide à Caesalpiniaceae pose évidemment des problèmes que les conditions écologiques actuelles, ni même la paléoclimatologie en ce qui concerne pour le moins les espèces littorales, ne peuvent résoudre; il faut préciser que ce site paraît absolument unique au Cameroun parmi les inselbergs intra-forestiers actuellement connus ou repérés sur photographies aériennes.

Un certain nombre d'observations géologiques et géomorphologiques, ± publiées à ce jour, viennent cependant apporter leur concours pour tenter d'émettre des hypothèses sur ces problèmes:

— la position de Nkoltsia, à seulement 35 km de la mer et se dressant sur la plaine littorale cristallophyllienne non sédimentaire de Kribi,

— la présence d'une faille importante au long de la côte atlantique, de Kribi à Campo (avec chutes de la Lobé près de Kribi à une quinzaine de mètres de hauteur directement au-dessus de la mer),

— l'existence des lacs Ossa près d'Edea (60–80 km NNW-Nkoltsia), eux-mêmes à 50 km de la mer, avec rivages extrêmement sinueux représentant d'anciens rias ou petits fjords à peine érodés, des arbustes de cordons littoraux se retrouvant sur leurs berges (*Manilkara obovata, Martretia quadricornis, . . .*),

— le bras de mer séparant l'île de Fernando Po de la côte camerounaise, large de 30 km et profond actuellement de 100 m seulement, exondé il y a 15000 ans (si l'on en croit des sources bibliographiques cependant imprécises),

— en bordure de mer, face à Fernando Po et à 150 km au NW de Nkoltsia, le Mont Cameroun, volcan encore actif (avec dernières émissions importantes de laves en 1959 et 1922, cette dernière à peine recolonisée par un taillis arbustif de quelques mètres de hauteur); pour ses 4 100 m (autrefois 4 070 m), il y aurait 2 000 m de laves basaltiques superposées et 2 000 m dus à la surrection du soubassement,

— la découverte (vers 1968), en place (P. Vincent, comm. pers.), sur les pentes méridionales du Mont Cameroun, vers 300 m d'altitude, de coquilles d'*Arca* très récentes,

— la nature sous-marine (P. Vincent, comm. pers.) des laves du petit volcan de Kumba, n'atteignant que 300 m de hauteur, au pied septentrional du Mont Cameroun,

— un ensemble de multiples failles formant un quadrillage ayant affecté toute la zone située à 100 km au Nord de Nkoltsia et à 100 km à l'Est du Mont Cameroun, avec des chaînons quartzitiques ainsi mis en relief.

Mouvements épirogéniques, mouvements tectoniques, répercussions volcaniques, conséquences hydrostatiques . . . tout ceci est bien mal daté mais la littérature fait état de mouvements tectoniques il y a 500 000 et 200 000–150 000 ans, tout en s'engageant aussi dans des chronologies paléoclimatiques où, à notre point de vue, il reste bien difficile — pour le Cameroun — de distinguer entre Tertiaire ancien, Pliocène, Pleistocène, Quaternaire très récent, . . .

La végétation de Nkoltsia correspondrait-elle à une période où une flore zambézienne se mélangeait sur la côte à une flore littorale? C'est là l'hypothèse de Villiers, bien difficile encore à étayer. Peut-être une recherche multidisciplinaire, avec participation de géologues, de géographes, de zoologistes même, voire de palynologistes, permettrait-elle d'apporter de nouveaux éléments pour 'comprendre Nkoltsia.' Il serait grand temps d'entreprendre cette étude d'ailleurs car le travail de Villiers révèle que la forêt dense humide à Caesalpiniaceae colonise actuellement peu à peu les paléoformations de cette originale colline.

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The woody vegetation communities of the Hluhluwe-Corridor-Umfolozi Game Reserve Complex

A. WHATELEY* and R. N. PORTER*

ABSTRACT

Land units for the 900 km^2 Hluhluwe-Corridor-Umfolozi Game Reserve Complex in north eastern Natal were identified on aerial photographs. The physiognomy, dominants and description of the woody vegetation for each unit were identified during ground inspections and, where necessary, the point-centred quarter method was applied. Two forest, two riverine forest, ten woodland and two thicket communities were recognized. These communities are described according to their distribution, height and percentage frequency of the components in the different canopy strata. A map at a scale of 1:25 000 was also compiled. Some of these communities are compared with other similar woodlands previously described for Natal. In some communities the frequency of certain dominant canopy species in the under tree strata was extremely low and autecological research has been suggested.

RÉSUMÉ

LES FORMATIONS VÉGÉTALES LIGNEUSES DES RESERVES DE FAUNE DE HLUHLUWE ET UMFOLOZI ET DE LA ZONE INTERMÉDIAIRE

L'interprétation des photographies aériennes des 900 km^2 des Réserves de faune de Hluhluwe et Umfolozi et de la zone intermédiaire dans le nord-est du Natal a permis de délimiter un certain nombre de formations végétales. La physionomie, les espèces dominantes et la description de la végétation ligneuse pour chaque formation ont été établies au cours de prospections de terrain, et lorsque cela se justifiait, la méthode 'point-centred quarter' a été appliquée. Deux types de forêts, deux types de forêts riveraines, deux types de forêts claires et deux types de fourrés ont été reconnus. Ces formations sont décrites suivant leur répartition, la hauteur et la fréquence exprimée en pourcentage des composantes des différentes strates de la voûte. Une carte à l'échelle de 1:25 000 a également été établie. Certaines de ces formations sont comparées avec d'autres forêts claires similaires décrites antérieurement au Natal. Dans certaines formations, la fréquence de certaines espèces dominantes de la voûte dans la strate arbustive était extrêmement faible et une recherche autécologique a été préconisée.

INTRODUCTION

The Hluhluwe-Corridor-Umfolozi Game Reserve Complex is a 900 km^2 area in central Zululand (28°00'S and 28°26'S; 31°43'E and 32°09'E) and comprises the Hluhluwe Game Reserve (225 km^2) in the north, the Umfolozi Game Reserve (447 km^2) in the south and an intervening area of state land referred to as the Corridor (227 km^2). The whole area, bounded by a game proof fence, is surrounded by KwaZulu where population densities are high and peasant agriculture is extensive (Fig. 1).

The Game Reserve Complex occupies the foothills of the first escarpment on the western side of the Zululand coastal plain. The terrain is broken by numerous hills and valleys and ranges in altitude from 60–750 m above sea level. Part of the catchment areas of four large river systems occur in the Complex: the Hluhluwe River with its two major tributaries, the Manzibomvu and Nzimane Rivers in the north, the Nyalazi River to the south and further south, the Black and White Mfolozi Rivers.

By far the largest area is covered by shales and sandstones of the Volksrust, Vryheid and Pietermaritzburg formations (Ecca series). Dolerite sills have intruded and are particularly extensive in the Corridor and Umfolozi Reserve. On the western boundary of the Corridor and Hluhluwe Reserve areas of dwyka tillite, table mountain sandstone and granite are found. The eastern part of Hluhluwe Reserve is covered mainly by shales and sandstones belonging to the Beaufort series and a small area of basalt lava is also present.

Swartland and Sterkspruit are the main soil forms associated with the Ecca areas, whereas extensive areas of Shortlands as well as Milkwood and Bonheim series are found on dolerite areas. Shallow Mispah soils also occur extensively.

Rain falls mainly between October and March. Hluhluwe Game Reserve has a greater mean annual rainfall (990 mm, n = 47) than Umfolozi Reserve (720 mm, n = 20) and the coefficient of variation for the two stations is 27,4% (n = 24) and 25,2% (n = 20) respectively. Temperatures are warm to hot, particularly during summer months. Very occasional frosts have been recorded in some river valleys.

The Game Reserve Complex lies within two veld types as described by Acocks (1953). Most of the area lies within the Lowveld subcategory of the Tropical Bush and Savanna Types and the remainder is Zululand Thornveld, a subcategory of the Coastal Tropical Forest Types. These areas correspond with bioclimatic subregions 9 and 10 as described by Phillips (1973).

Archaeological evidence indicates that man has occupied these areas more or less continuously for the last half million years (Penner, 1970). Both the vegetation and fauna were modified by Iron Age inhabitants. Following the thinning of woody plant cover for cultivation and fuel needs, fire was an important factor in maintaining the open nature of the vegetation that existed at the time of proclamation of the two game reserves in 1895 (Hall, 1979;

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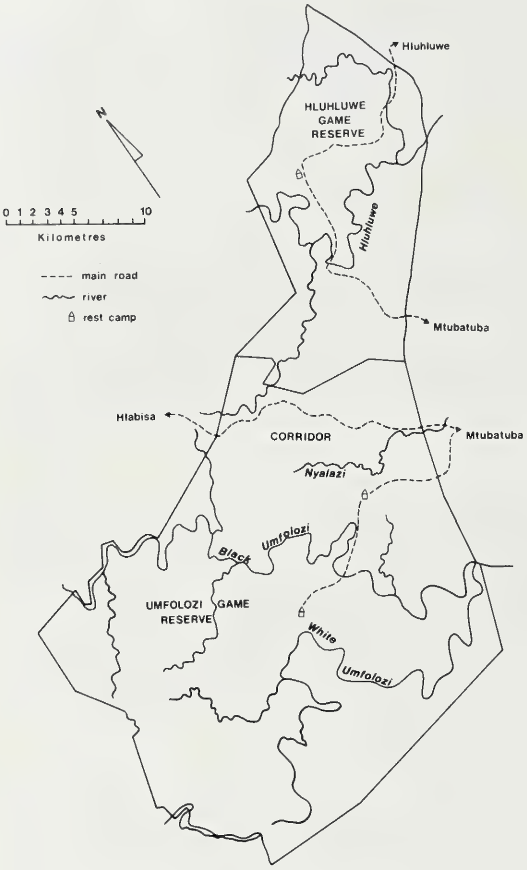

FIG. 1.—Hluhluwe-Corridor-Umfolozi Game Reserve Complex.

Feely, 1978). The fire history of this area has been the subject of a detailed investigation (Berry & Macdonald, 1979) and a widely held opinion is that the woodlands of the Game Reserve Complex are ‘derived’ as a result of the actions of man and/or fire. Other impacts on the vegetation occurred during the anti-nagana campaign (1942–1946) when certain specific areas were bush cleared (Mentis, 1970). The largest was a 3,2 km wide strip along the western boundary of Umfolozi Game Reserve between the White and Black Mfolozi Rivers. A large variety of animal species are found in the area (Bourquin *et al.*, 1971), including large herbivores.

METHODS

The vegetation of Hluhluwe Game Reserve was first mapped by Henkel (1937) at a scale of 1: 31 680. Subsequently, both Ward (1961) and Downing (1972) compiled preliminary physiognomic maps. The vegetation of Umfolozi Game Reserve was first classified and mapped by Downing (1972) at a scale of 1:50 000. A more detailed map of the woody vegetation communities occurring in the entire Game Reserve Complex was required. It was intended that the map should be used as an aid in management planning and would also be useful for other biological research projects. We aimed to compile a map at a scale of 1: 25 000 of the woody plant communities occurring in the Game Reserve Complex. Accompanying the map would be a description of the various communities that were recognized.

The various landscape units were first identified on aerial photographs. Field work was extensive in order to fix the boundaries of the various plant communities. Point centred quarter transects were set up and located within representative examples of each community. Recording points were 20 paces apart in the forest and woodland communities, but 10 paces separated these positions in the thicket communities. At each recording point the nearest woody plants in two height classes growing in each quarter segment were identified and recorded. Woody plants greater than 2 m in height and plants between 0,3 m and 2 m in height were recorded separately for each plant community except for the forest communities, where plants were recorded according to their canopy strata.

RESULTS

The physiognomy of the vegetation in this part of Zululand can be variously described as forest, savanna woodland, savanna (various types) and thicket (Anon., 1956) or as woodland, wooded grassland, bushland thicket and induced types (Pratt *et al.,* 1966; Greenway, 1973). An alternative classification of Phillips (1973) would give the following physiognomic types: forest, woodland, open woodland, thicket and grassland. The classification of Phillips (*l.c.*) was adopted for this study with one modification: an induced thicket category as described by Pratt *et al.* (1966) was included.

Two forest, two riverine forest, ten woodland, one thicket and one induced thicket communities were recognized as being present in the Game Reserve Complex. These different communities are described below and in Tables 1–5. Percentage cover and canopy heights for the different woodland communities are given in Table 5.

Celtis africana – Harpephyllum caffrum *Forest*

This forest is found on the high hills in the north-western part of Hluhluwe Game Reserve, where it covers extensive areas on south-facing hill slopes (Fig. 2). These hills are steep-sided, incised by many dry, rocky water courses and rise to 570 m above sea level. Relic patches of forest are also found at a few isolated, small localities in the Corridor state land, but do not occur south of the Black Mfolozi River. This forest provides a suitable habitat for many different fauna species of tropical origin.

Three distinct canopy strata are readily distinguishable (Tables 1 & 2). The upper canopy reaches an average height of 15 m with a ceiling height of 9–12 m. The mid canopy has an average height of 7 m with an average ceiling height of 4 m. The under stratum consists of plants usually less than 2 m in height. *Ficus natalensis* and *Harpephyllum caffrum* are the largest trees in the forest with the former species being associated with drainage courses. The

TABLE 1. – Species with a recorded frequency of greater than 5% for the forest and riverine forest communities

SPECIES	FOREST						RIVERINE FOREST			
	Celtis africana – Harpephyllum caffrum			Celtis africana – Euclea schimperi			Ficus sycamorus – Schotia brachypetala		Spirostachys africana – Euclea schimperi	
	Upper	Middle	Lower	Upper	Middle	Lower	>2m	0,1–2m	>2m	0,1–2m
Acacia robusta				+	–	–	6,7	8,4	3,0	1,3
Acalypha glabrata	–	6,8	11,6	–	5,6	23,2	7,2	23,8	2,9	4,9
Azima tetracantha							+	5,4		
Bequaertiodendron natalense	–	15,8	11,8							
Berchemia zeyheri	+	–	–	22,1	3,3	–			+	+
Bersama lucens	–	+	6,2	–	1,2	1,6				
Calpurnia aurea	+	6,0	11,3	–	7,7	3,6				
Cassine aethiopica	1,4	+	–	9,9	3,1	–	+	+	2,5	+
Celtis africana	20,4	3,4	2,3	8,9	2,3	3,9				
Chaetacme aristata	5,1	3,2	+	+	1,8	2,7			+	–
Cola natalensis	–	4,9	11,6	–	5,0	5,0				
Combretum kraussii	11,0	+	+	–	+	1,5				
Commiphora harveyi	+	–	+	11,3	+	1,2	–	–	+	+
Croton menyhartii							–	2,3	+	8,4
C. silvaticus	4,4	2,3	5,5	–	+	+				
Diospyros glandulifera					1,6	7,2	–	2,3	3,7	3,0
D. simii				–	–	5,0	–	+	–	+
Ehretia rigida	–	+	+	–	1,2	5,6	–	1,2	+	8,5
Erythroxylum emarginatum	–	10,7	6,7	–	3,8	1,8	+	+		
Euclea natalensis	+	+	5,9	+	+	3,3	–	1,2		
E. schimperi	–	–	+	22,6	14,6	10,0	2,8	8,9	10,5	16,7
Maytenus heterophylla	+	8,2	1,3	+	10,3	2,5	1,8	+	17,5	1,5
Olea africana							+	–	9,5	3,0
O. capensis	10,4	2,0	–	–	3,8	+				
Phoenix reclinata							5,4	4,9		
Plectroniella armata				+	+	–	5,7	3,5	3,6	1,8
Schotia brachypetala				7,0	+	+	9,6	–	4,8	–
Spirostachys africana				1,6	+	+	9,3	4,9	13,7	12,1
Strychnos decussata	3,6	3,8	6,3	+	2,4	3,9	+	–		
Teclea gerrardii	6,6	3,1	+	–	1,5	1,2				
TOTAL	62,9	70,2	80,5	83,4	69,2	83,2	48,5	66,8	71,7	61,2
N.		912			742		392		580	

forest is a mixed evergreen-deciduous community with major species such as *Celtis africana, Croton sylvaticus, Combretum kraussii* and others losing their leaves, whereas other species such as *Harpephyllum caffrum, Protorhus longifolia, Ficus natalensis, Olea capensis, Albizia zuluensis* and others, remain evergreen. *Celtis africana* is the dominant species in the upper tree stratum and has a frequency of 20,4%. For the upper, middle and lower canopy strata some 43, 49 and 42 species were recorded respectively and for both the upper and middle strata only 5 species had a frequency of 5% or greater.

Some of the forest margin species do not occur in the interior of the forest. Trees and shrubs which appear to be exclusive to the forest margin are: *Ximenia caffra, Psychotria capensis, Dombeya burgessiae, Cussonia spicata, Canthium ventosum, Rhus pentheri* and *Diospyros dichrophylla.*

Lianas are abundant in the canopy. Some common species are *Dalbergia armata, D. obovata, Entada spicata, Rhoicissus tomentosa, R. rhomboidea* and *Acacia ataxacantha.* Dense stands of *Isoglossa delicatula* are associated with those areas where the upper canopy strata are interrupted. Thicket patches of *Acalypha glabrata* and of *Calpurnia aurea* also occur. Cliffs and rocky outcrops with associated scree slopes occur in a number of localities within this forest community. Here *Strychnos decussata* and *Commiphora harveyi* are common associates. Growing on the forest floor are seedlings of various tree species, some fern species, the grass *Oplismenus hirtellus* and *Cyperus albostriatus.*

Celtis africana–Euclea schimperi *Forest*

This forest covers fairly extensive areas in north and north eastern Hluhluwe Game Reserve between the 120 and 300 m contours (Fig. 2). Small relic patches are found in Umfolozi Game Reserve and in the Corridor. The community is mostly associated with the relatively moister south and south east hillsides.

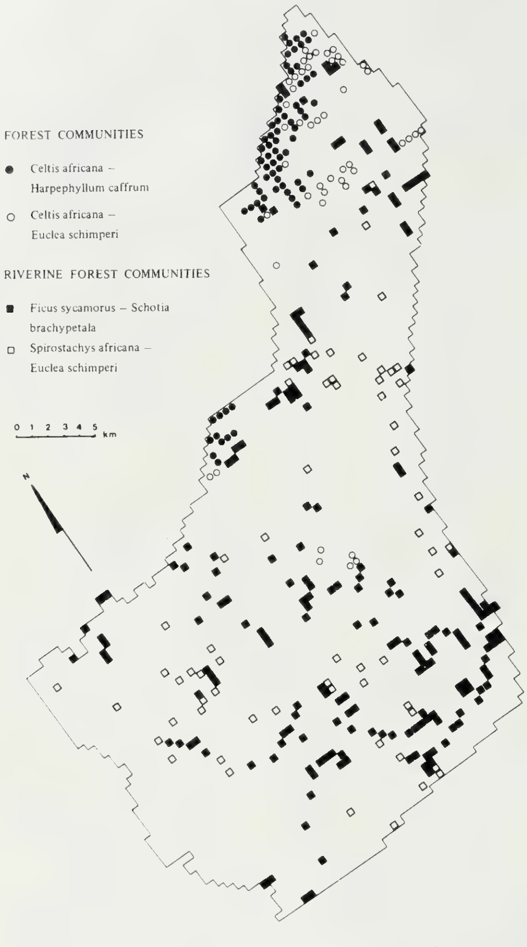
FOREST COMMUNITIES
● Celtis africana – Harpephyllum caffrum
○ Celtis africana – Euclea schimperi
RIVERINE FOREST COMMUNITIES
■ Ficus sycamorus – Schotia brachypetala
□ Spirostachys africana – Euclea schimperi
0 1 2 3 4 5 km
N

FIG. 2.—Forest and riverine forest communities.

Three distinct canopy strata are distinguishable (Tables 1 & 2). The upper canopy reaches 9 m and has an average ceiling height of 6 m. The mid canopy has an average height of 6 m, but usually merges with the upper canopy. The ceiling height varies between 2 and 3 m above ground level and coincides with the canopy of the under stratum. *Euclea schimperi* and *Berchemia zeyheri* were found to be the most abundant species in the upper stratum with a percentage frequency of 22,1 respectively. For the upper, middle and lower canopy strata some 33, 61 and 40 species were recorded respectively and for the upper stratum only 6 species had a frequency of 5% or greater.

This mixed deciduous-evergreen forest community is closely allied to the *Celtis africana—Harpephyllum caffrum* Forest in terms of its general location, distribution and tree species present. However, it is a drier form of forest, being found at lower altitudes.

Ficus sycamorous — Schotia brachypetala *Riverine Forest*

This riverine forest is confined to the banks of the larger rivers and their major tributaries in the area where extensive, but narrow stands are to be found (Fig. 2.)

Three canopy strata are readily distinguishable (Tables 1 & 2). An upper canopy, often discontinuous, with a height varying between 15 and 20 m and having a ceiling height of between 6 and 10 m, is present. The mid canopy is between 8 and 10 m in height with an average ceiling height of 3,5 m. Often merging into the mid canopy is an under canopy varying in height between 3 and 4 m. The herbaceous layer consists of both stoloniferous and tufted grass species, shrubs and other woody plants. Because of its size, *Ficus sycamorus* is the most prominent tree, but *Schotia brachypetala* has the highest frequency of 9,6%. Some 59 and 48 species were recorded in height categories greater and less than 2 m respectively. This riverine forest community is well utilized by herbivores and is particularly important as a food source during the dry winter months.

Spirostachys africana — Euclea schimperi *Riverine Forest*

The *Spirostachys africana — Euclea schimperi* Riverine Forest community occurs throughout the area as a narrow strip along seasonal water courses throughout the whole game reserve complex (Fig. 2).

Three canopy strata are distinguishable (Tables 1 & 2). An upper canopy reaching a height up to 8 m with an average ceiling height of 3,5 m, is present. The mid canopy has an average height of 4,5 m and an average ceiling height of 2,3 m. Often merging into the mid canopy is an under canopy varying in height between 2 and 3 m.

The most frequent species greater than 2 m in height were *Spirostachys africana* at 13,7% and *Euclea schimperi* at 10,5%. Some 64 species were recorded for plants greater than 2 m in height and 53 species that were below the 2 m height were found.

The herbaceous layer consists mainly of tufted perennial grass species. Many small shrubs also occur.

Spirostachys africana *Woodland*

The *Spirostachys africana* Woodland covers extensive areas in all bottomland situations in the Umfolozi Game Reserve, particularly in the catchments of seasonal water courses. It is not found in the Corridor and has only a limited distribution in Hluhluwe Game Reserve, being found in riverine terraces along the Hluhluwe and Nzimane Rivers (Fig. 3).

Species composition is variable and this community probably consists of numerous different associations and no distinction has been made between them. However, a major difference is in the presence or absence of *Acacia grandicornuta*. This species is a common associate of this woodland in the Umfolozi Game Reserve, but is absent in Hluhluwe Reserve. *Spirostachys africana*, with a frequency of 27,2% in the upper tree stratum, and 21,5% in the under stratum, was found to be dominant (Table 3). A total of 32 plant species in the upper tree stratum and some 29 species less than 2,0 m in height were recorded, having a frequency of less than 5% (Table 4).

TABLE 2.—Species with recorded frequencies of less than 5% for the forest and riverine forest

SPECIES	FOREST: Celtis africana – Harpephyllum caffrum: Upper	Middle	Lower	Celtis africana – Euclea schimperi: Upper	Middle	Lower	RIVERINE FOREST: Ficus sycamorus – Schotia brachypetala: >2m	0,1–2m	Spirostachys africana – Euclea schimperi: >2m	0,1–2m
Acacia burkei							+	–		
A. grandicornuta							+	–		
A. karroo							–	0,5	0,2	–
A. nigrescens									0,7	–
A. nilotica							–	0,7	2,3	1,5
A. schweinfurthii							2,1	+		
Acalypha sonderiana	–	0,3	0,3	–	4,9	–			+	0,6
Acokanthera oppositifolia				–	+	–	–	+		
Albizia versicolor							+	–	+	–
A. suluensis	3,6	–	–							
Allophylus natalensis									+	–
Antidesma venosum							0,8	–		
Apodytes dimidiata	+	0,2	+							
Asparagus falcatus									–	2,7
A. macowanii							–	+		1,7
A. saundersiae										1,8
A. **setaceus**										0,6
A. sp.										
Austromimusops marginata	1,4	4,2	0,5	–	0,5	–				
Brachylaena ilicifolia									2,0	3,5
B. uniflora	1,1	–	–							
Bridelia micrantha	0,3	–	–				0,5	–		
Canthium ventosum	–	1,2	–	–	+	–			+	–
C. sp.							0,5	–		
Capparis sepiaria									–	0,2
Carissa macrocarpa	–	0,2	0,7							
Cassine transvaalensis									0,5	+
Clausena anisata	–	–	0,4	–	–	0,6			–	+
Clerodendrum glabrum	2,4	–	0,3	–	+	+				
Combretum molle				0,8	0,8	–	–	+	0,5	–
Commiphora woodii	0,5	–	+							
Cordia caffra	2,0	+	–	+	3,9	3,2			+	–
Cussonia spicata				0,6	+	–			+	–
C. zuluensis				+	+	–			0,3	–
C. sp.	–	+	–						0,7	–
Dalbergia armata									0,6	2,3
D. obovata							+	–	0,5	+
Dichrostachys cinerea							0,5	1,4	0,7	0,6
Dinocanthium hystrix									0,5	–
Diospyros lycioides	–	+	0,3	–	0,6	–	3,1	4,7		
D. natalensis	+	3,2	3,5	–	+	–				
D. whyteana									0,7	0,2
D. sp.							1,0	2,8		
Dombeya burgessiae	–	0,7	0,9	–	+	–				
D. cymosa				0,8	1,5	2,9	+	+	1,1	+
D. rotundifolia				+	0,4	–			0,7	–
Dovyalis caffra							+	+		
D. rhamnoides	–	0,6	0,9	–	+	0,7				
Drypetes arguta	1,3	4,6	+	–	+	–				
D. gerrardii	–	2,1	2,6							
Ekebergia capensis	0,7	0,2	+	+	0,4	–				
Erythrina lysistemon	+	–	–	0,6	+	–			+	–
Euclea divinorum							+	–	1,0	0,5
E. natalensis									0,2	0,8
E. undulata							–	0,9		
Eugenia natalitia	0,2	0,8	0,4						+	0,2
Euphorbia tirucalli							+	–	1,1	0,2
E. sp.	+	–	–							
Fagara capensis	0,2	0,2	+	+	+	+	+	0,5	0,2	–
F. davyi				–	–	+			–	+
Ficus capensis	+	–	–						+	–
F. natalensis	2,5	–	–	+	–	–				
F. sycamorus							3,4	–		
F. sp.							1,5	0,9		
Galpinia transvaalica	0,3	+	–	2,8	1,5	0,4	1,0	–	1,3	+
Gardenia amoena	–	0,5	0,7	–	+	–			0,3	1,0
Grewia caffra	–	–	0,8	–	+	1,0			–	0,2
G. sp.									–	0,2
Harpephyllum caffrum	4,3	0,3	–	1,0	+	–			0,2	–
Heteropyxis natalensis				+	–	–	1,3	–		
Hippobromus pauciflorus	–	+		+	+	1,6	+	0,9	+	1,0
Kraussia floribunda				–	–	0,7	0,8	1,4	0,2	1,0
Maerua rosmarinoides									0,2	–
Manilkara concolor							0,5	+		
M. discolor	1,9	0,2	–							
Maytenus senegalensis							1,3	2,6	0,2	0,2
Mimusops caffra				–	3,7	+	0,5	0,5	1,7	1,5
M. obovata	2,0	0,3	–	0,6	0,5	+	0,5	–	0,6	0,6
Nuxia floribunda									0,5	–
N. oppositifolia							3,1	1,9	0,2	–
Ochna arborea							–	+		
O. natalitia				–	1,9	1,9			0,5	1,7
Ozoroa engleri									0,2	–
Pappea capensis							3,1	–	0,8	–
Peltophorum africanum				+	–	–				
Phyllanthus reticulatus				+	0,7	–	+	0,5	+	+
Protorhus longifolia	3,0	–	–							
Psychotria capensis	–	+	–							
Ptaeroxylon obliquum	0,2	–	–							
Rawsonia lucida	–	0,2	0,8							
Ricinus communis							0,5	0,9		
Rhus chirendensis	1,8	0,3	+				3,6	0,7	0,2	1,0
R. natalensis							2,8	–		
R. pentheri	–	–	0,3	–	0,5	0,6	+	+	0,5	0,2
Rothmannia globosa	–	0,3	0,4	–	+	–				
Schotia capitata							2,1	0,5		
Sclerocarya caffra	0,3	–	–	0,8	–	–	0,8	+	0,2	
Scolopia zeyheri	2,5	0,6	+	–	+	0,9			+	0,2
Sideroxylon inerme	–	+	–	2,8	0,9	–	2,3	0,9	1,5	0,2
Strychnos henningsii	1,5	1,5	2,0	–	0,4	–			–	+
S. madagascariensis									+	–
S. spinosa							+	–		
Syzygium cordatum							1,8	0,9		
S. guineense							0,5	–		
Tarchonanthus camphoratus				–	+	–	+	–		
Tecomaria capensis						1,0	–	0,7		
Thespesia acutiloba							0,5	–		
Trichilia emetica	0,4	–	–				0,8	–		
Trimeria grandifolia	0,4	1,2	0,3							
Turraea floribunda	–	1,0	–	–	+	–				
T. obtusifolia							+	–		
Urera tenax				–	–	+				
Vangueria infausta							+	–		
Xeromphis obovata				–	+	–	–	0,5	0,3	0,5
Ximenia caffra									–	+
Ziziphus mucronata	–	+	–	1,0	+	–	1,8	2,1	0,7	–
Unknown	+	–	–	–	1,5	0,4	1,0	1,9	0,8	4,0

TABLE 3.—Species with a recorded frequency of greater than 5% for the woodland and thicket communities

SPECIES	WOODLAND																				THICKET		INDUCED THICKET	
	Acacia burkei		A. gerrardii		A. karroo		A. nigrescens		A. nilotica		A. tortilis		Combretum apiculatum		C. molle		Euclea divinorum		Spirostachys africana		Acacia caffra		A. karroo – Dichrostachys cinerea	
	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m
Acacia burkei	19,0	4,6	+	–					+	+	1,2	–	1,5	0,5	2,0	2,8	1,3	–	1,3	–			+	+
A. caffra	+	+	+	4,1	12,5	3,7			1,4	5,1			–	1,0	+	–	–	+			46,7	27,0	2,0	+
A. davyi																								
A. gerrardii	2,0	+	20,2	4,8					+	–	+	+	4,5	0,2	1,4	–	+	–	+	–				
A. grandicornuta	+	–	+	–			5,0	–					0,2	–					11,2	1,5				
A. karroo	3,9	2,4	4,5	17,3	60,4	15,2			9,3	9,1	+	+	0,2	0,2	6,2	1,4	1,6	1,8			3,5	+	44,2	31,0
A. nigrescens							55,0	4,1			4,5	1,5	11,2	4,7					+	–				
A. nilotica	8,1	3,7	15,7	4,6	2,6	+	+	5,1	60,9	25,4	2,7	+	0,5	1,7	1,4	3,5	9,7	9,1	3,8	3,5	1,8	3,8	19,1	10,3
A. tortilis	+	+	2,0	1,5			9,5	19,4	+	–	57,0	29,1	2,0	2,0			+	–	+	+				
Azima tetracantha			–	+							1,2	25,5					–	+						
Berchemia zeyheri	+	+	1,2	+	–	5,2			+	2,2			1,2	–	–	2,8	2,4	+	+	–			+	+
Combretum apiculatum													31,0	0,7										
C. molle	9,4	2,7	+	–					+	–			0,2	–	25,3	4,2	+	+			2,6	3,4	+	+
Commiphora neglecta	–	+	–	1,3			2,0	10,2			–	1,3	1,2	0,5										
Croton menyhartii													–	5,7					+	9,1				
Dalbergia obovata	+	+			–	+			–	2,2					–	6,3					–	+		
Dichrostachys cinerea	12,8	20,8	3,7	8,4	9,4	9,4	+	13,3	10,8	25,3	4,0	1,8	3,2	19,2	8,2	8,4	8,1	15,8	+	2,1	24,2	20,7	17,0	23,5
Diospyros dichrophylla	+	3,9	–	3,3	–	3,7			–	+							–	+			–	8,4	–	2,7
D. glandulifera	+	1,3											–	6,0			–	+	+	–	2,6	–	+	+
D. lycioides	–	+			1,6	7,3					+	1,3	–	0,2										
Dombeya rotundifolia	2,6	2,2	+	–					+	–			–	1,5	2,7	11,2	+	–			10,6	8,9	1,1	+
Ehretia rigida	–	1,9	+	1,8					–	+	+	5,4	–	2,5	–	4,9	+	5,1	–	8,0	–	+	–	+
Euclea crispa	–	+			–	10,5			–	+							–	+	–	+	+	+	–	3,0
E. divinorum	+	2,2	5,2	7,1	–	2,1			2,3	1,8	–	1,5			4,8	–	40,5	14,9	8,3	13,6			+	+
E. natalensis	–	1,2	–	+	–	1,6	–	+	–	2,3	–	+	0,2	6,0			–	2,7	–	2,4			–	+
E. schimperi	+	1,2	4,7	4,0	2,1	–	–	+	1,6	2,3	–	+	0,2	1,7	8,2	2,1	9,7	7,1	4,0	8,0	+	1,3	+	+
Grewia occidentalis			–	+			–	7,1																
G. subspathulata													6,2	9,5										
Hippobromus pauciflorus	1,2	1,2											6,7	8,5	+	1,4	2,1	2,4	5,3	3,2	+	5,5	+	1,8
Maytenus heterophylla	+	1,3	7,0	1,5	–	+	2,5	5,6	+	4,3	1,2	3,1			1,4	2,8	2,2	3,1	+	–	1,3	3,4	6,6	7,2
M. senegalensis	4,0	4,8	–	3,3	3,1	4,7	–	6,1	2,1	6,4	6,5	11,9			–	7,7	–	+					–	+
Rhus pentheri	2,9	1,9	5,5	9,7	3,1	5,2			3,1	2,9	–	1,8	0,7	0,5	4,1	3,5	5,2	3,3	–	+			1,3	1,4
Spirostachys africana	+	1,8	+	+			–	4,0			2,2	+	8,2	4,2	–	1,4	1,9	6,7	27,2	21,5			+	+
Tarchonanthus camphoratus			3,0	7,1			4,5	11,2	+	+	1,2	3,6	–	0,5	17,8	8,4	+	1,6	–	2,6				
Ziziphus mucronata	1,8	1,1	7,7	2,0	–	+	4,5	4,1	+	1,3	3,7	+	2,5	2,0	+	+	1,8	1,8	4,2	+	+	+	+	2,0
TOTAL	67,7	60,2	80,4	81,8	94,8	68,6	83,0	90,2	91,5	90,6	85,4	86,8	81,6	79,5	83,5	72,8	86,5	75,4	65,3	75,5	93,3	82,4	91,3	82,9
N.	1304		400		192		200		868		100		400		144		676		692		240		1344	

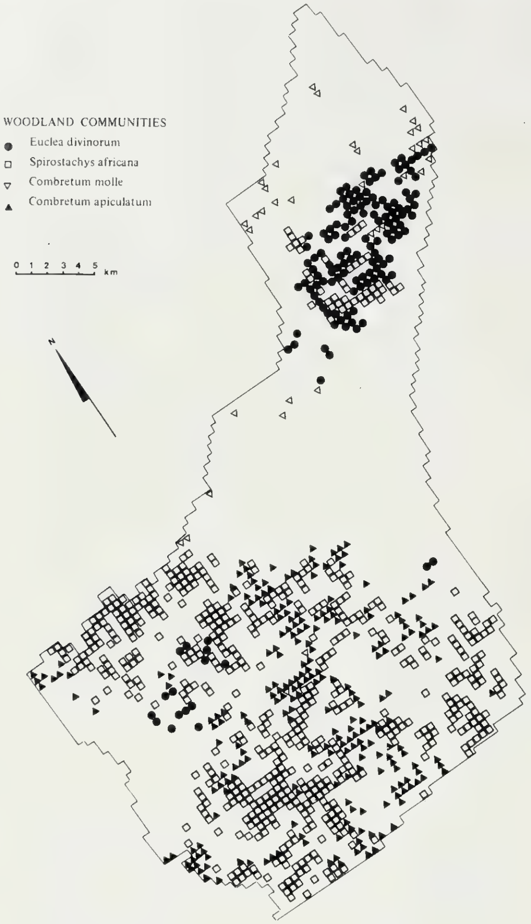

FIG. 3.—Woodland communities.

The herbaceous layer consists of a variable mixture of shrubs and grasses. Where tree canopy cover is dense, the grasses are stoloniferous, but where breaks in the tree canopy occur, various tufted perennial grasses are found.

Combretum apiculatum *Woodland*

Combretum apiculatum Woodland has a restricted distribution, occurring on rocky hillsides in Umfolozi Game Reserve (Fig. 3). Species composition is variable, probably depending on local edaphic and climatic differences. *Combretum apiculatum* is the dominant species and characterizes this community. In the upper tree stratum it has a percentage frequency of 24,0 (Table 3).

Some 31 species were recorded in the upper tree stratum and 48 species, being less than 2,0 m in height, having a frequency of less than 5% (Table 4).

This deciduous community of irregular shaped trees has a highly variable canopy cover due to variations in tree density. Where trees are clumped, the canopy cover lies between 50 and 75%, whereas the more usual situation is for trees to be well separated and with a canopy cover between 10 and 25%. An under stratum of very widely separated plants of usually less than 2 m in height, is present.

A grass sward of medium to tall tufted perennial species is characteristic of the herbaceous layer. Fires penetrate this community and are often of high intensity.

Combretum molle *Woodland*

Combretum molle Woodland is an uncommon plant community in the area occurring mainly to the north of the Hluhluwe River. It occurs on steep, rocky hill slopes between 180 and 300 m a.s.l. (Fig. 3). The dominant woody species characterizing this community were found to be trees of *Combretum molle* with a frequency of 25,3% in the upper tree stratum and *Dombeya rotundifolia* with a frequency of 11,2% in the under stratum (Table 3). Another 21 species were recorded in the upper tree stratum and 24 species being less than 2,0 m in height, having a frequency of less than 5% (Table 4). As grass sward of short tufted perennial species is characteristic of the herbaceous layer. Fire penetrates this community on occasions, particularly in years of above average rainfall.

Euclea divinorum *Woodland*

Euclea divinorum Woodland covers extensive areas on gently sloping ground in the Hluhluwe River Valley, particularly below the 200 m contour (Fig. 3). It is scarce elsewhere.

The dominant species characterizing this community is *Euclea divinorum,* having a frequency of 40,5% in the upper tree stratum. In the under stratum *E. divinorum* and *Dichrostachys cinerea* have frequencies of 14,9% and 15,8% respectively (Table 3). Another 35 species were recorded in the upper tree stratum and 39 species being less than 2,0 m in height, having a frequency of less than 5% (Table 4).

Under tree canopies, the grass sward is mainly stoloniferous. Where there is a break in the canopy or it is less dense, tufted perennial grasses occur. Generally fires only rarely occur with penetration, being confined to marginal areas only.

The community is commonly found growing on margalitic soils. Common soil series include Bonheim, Glengazi and Dumasi. Both sheet and gulley erosion is a common feature in this community.

Acacia karroo *Woodland*

Acacia karroo Woodland is largely confined to river valleys in the north-eastern part of Hluhluwe Game Reserve (Fig. 4). It occurs on steep hillsides up to approximately 300 m above sea level.

Acacia karroo was found to be the dominant species characterizing the community, with a frequency of 60,4% in the upper and 15,2% in the under tree strata (Table 3).

Another 9 woody plant species were recorded in

TABLE 4.—Species with a recorded frequency of less than 5% of the woodland and thicket communities

SPECIES	ACACIA WOODLANDS												OTHER WOODLANDS								THICKET		INDUCED THICKET	
	A. burkei		A. gerrardii		A. karroo		A. nigrescens		A. nilotica		A. tortilis		Combretum apiculatum		C. molle		Euclea divinorum		Spirostachys africana		Acacia caffra		Acacia karroo–Dichrostachys cinerea	
	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m	>2m	0,1–2m
Acacia borleae			0,2	3,6													–	0,7	+	–				
A. kraussiana															–	1,4								
A. robusta	2,5	0,3							+		3,0	0,5			–	4,2	0,3	0,4			+	0,8	0,5	0,6
A. senegal	–	0,2	1,7	1,0					–	+	0,2	–	0,2				–	0,4	+	+				
Acalypha glabrata	–	+																						
A. sonderiana	+	–																						
Albizia adianthifolia	0,5	0,2																						
A. versicolor	3,3	0,8																			1,3	+	+	0,3
Aloe marlothii	+	–												0,7			1,0	0,9						
A. sp.	–	+																					–	+
Antidesma venosum	1,2	0,4																			+	–	+	–
Asparagus falcatus	–	0,8															–	0,4						
A. macowanii	–	0,3			–	0,5											–	1,5					–	+
A. setaceus	–	0,3			–	1,6											–	+						
A. sp.	–	+																				0,8	–	+
Boscia albitrunca	0,2	–	0,7	–			1,0	–			0,7	0,5	0,7						+	–				
Brachylaena discolor	+	0,9																						
B. ilicifolia	+	–	3,5	4,3					–	+	0,7	–					0,4	1,3	1,1	0,6				
Bridelia micrantha															0,7	–								
Canthium ventosum	0,3	0,7			–	1,6																		
C. sp.	–	+																						
Capparis sepiaria																	–	0,3						
C. tomentosa			–	+																			–	0,2
Carissa bispinosa																			–	+				
Cassine aethiopica	0,3	+											0,2	0,5			1,0	+	2,8	0,6				
C. transvaalensis			0,5	–			1,0	–					0,2				0,3	–	0,8	0,6			–	0,2
Celtis africana															0,7	–								
Chaetacme aristata	0,4	0,3																						
Clutia sp.															–	2,1								
Commiphora pyracanthoides							0,5	–																
Cordia caffra					1,6	1,0			1,0	0,5					2,7	–	0,6	0,6					1,1	+
Cussonia spicata	+	+							+	–			–	0,2							+	–	+	–
C. zuluensis													0,2	0,2										
Dalbergia armata					–	0,5																		
Dinocanthium hystrix																			+	1,2				
Diospyros simii	–	+											–	0,5	–	1,4	–	2,1					–	+
D. villosa									–	2,2			–	0,5							–	+	–	0,7
D. whyteana	+	+							–	0,2														
D. sp.	–	1,3	–	+	–	4,7			+	1,6					4,1	4,2	0,1	0,9	–	1,8	–	2,1	–	1,0
Dombeya burgessiae					–	0,5																		
D. cymosa													1,0	0,2					1,5	–				
Dovyalis caffra	+	0,6					1,0	–	+	–	0,2	1,3					–	0,4	2,1	4,1			+	+
D. rhammnoides	–	0,4																						
Ekebergia capensis	+	–																			+	+		
Erythrina latissima																							0,4	–
Euclea undulata											0,5	–					0,4	–	3,4	4,7				
Eugenia natalitia	–	3,7			–	1,6			–	+							–	0,9					–	+
Euphorbia tirucalli	+	–																						
Fagara capensis	+	1,6			–	3,1			–	+			–	0,2					–	+			–	0,3
F. davyi			–	0,5															–	+				
Ficus soldanella													0,5											
F. stuhlmannii	0,5	+							+	+													0,4	–
F. sp.	–	+							–	+													–	0,2
Galpinia transvaalica	+	–							+	–			5,2	1,0	–	2,1	0,1	–						
Garcinia livingstonei	+	–							–	+														
Gardenia amoena															–	0,7								
G. spatulifolia	0,4	+	0,2	–			2,0	1,5			0,2	–	–	0,7										
Grewia bicolor	–	1,4					1,0	4,6																
G. caffra	–	2,3	–	0,5																				
G. monticola			–	0,5									–	1,0					–	0,7				
G. villosa							–	2,0																
G. sp.	0,5	0,7	–	1,0	–	2,1	2,0	–			–	1,0			–	0,7	–	1,2	–	1,5			–	+
Heteropyxis natalensis	+	0,2													0,7	–					–	2,1		
Iboza riparia	–	0,2																						
Jasminum multipartitum			–	+									0,5	2,7										
Kigelia africana																							+	–
Kraussia floribunda	+	0,4			0,5	1,6			+	0,3							0,1	1,5			+	–	+	0,2
Lippia javanica	+	2,6																			–	2,5	–	1,6
Maerua angolensis			0,2	–							0,2	–												
M. rosemarinoides			–	+																				
Mimusops caffra														1,2			0,1	–	–	0,6				
M. obovata													0,2	1,0					–	+				
Mundulea sericea	1,0	+							–	+													+	–
Ochna natalitia	0,4	3,8															0,1	0,4						
Ormocarpum trichocarpum	+	–	0,2	+							–	+	–	0,2			–	0,7			–	0,8	–	0,8
Ozoroa engleri	0,2	0,2							+	+			1,2	–										
Pappea capensis			1,0	–			1,0	–			0,2	–	0,5	–			0,1	–	1,1	–				
Peltophorum africanum	2,8	1,0							–	+					0,7	0,7	0,9	–	+	–				
Phyllanthus burchellii	–	+																						
P. reticulatus	–	0,3							–	0,5											–	+		
Plectroniella armata	1,1	2,5	0,7	0,8							0,7	2,1	3,0	1,0			0,4	0,3	0,8	+				
Protea multibracteata	+	–																						
Rhus chirendensis	–	+																						
R. dentata	–	0,2									–	0,8												
R. fraseri					–	0,5															+	–	–	+
R. gueinzii													–	5,5										
R. natalensis	+	–	0,5	0,5			–	1,0			0,2	0,8					0,1	+	0,4	–				
R. rehmanniana	–	+			0,5	–			+	0,8													–	0,7
R. simmii														0,5										
R. sp.	–	+							–	0,8					2,0	–	0,1	–			–	1,3	+	+
Schotia brachypetala	0,5	+	1,7	–					+	0,2			0,7	–	0,7	0,7	1,6	0,4	4,9	+			0,4	–
S. capitata											0,7	–					0,3	–	2,1	–				
Sclerocarya caffra	2,3	0,2	0,2	–	–	0,5			2,1	0,2			0,2	–	0,7	–	1,3	–	+	–	+	–	2,2	0,3
Sclopia zeyheri																							–	0,4
Sideroxylon inerme	0,3	–	1,2	0,5	0,5	0,5	1,0	–	0,7	+	0,5	–	–	0,2	0,7	1,4	1,3	–	3,4	–				
Strychnos decussata	0,3	0,3																						
S. madagascariensis	1,3	0,4											1,5	–										
S. spinosa	1,7	0,6											0,5	0,2							–	+	0,3	0,2
Syzygium cordatum	+	–																					+	–
Tarchonanthus trilobus	2,9	1,6																						
Tecomaria capensis					–	0,5																		
Terminalia phanerophlebia													1,0	–										
Thespesia acutiloba			0,5	+							0,2	–							+	–				
Trema orientalis	–	+																						
Trichilia emetica	+	–																						
Vangueria infausta	0,2	+																						
Xeromphis obovata									–	0,5			–	0,2			0,1	1,0					–	0,2
Ximenia caffra	0,3	0,6	–	+					–	0,7					2,7	0,7							+	+
Unknown	0,4	1,1			2,1	4,2			–	2,1			–	1,0	–	4,2	0,3	4,0	0,8	2,9	–	1,7	+	0,9

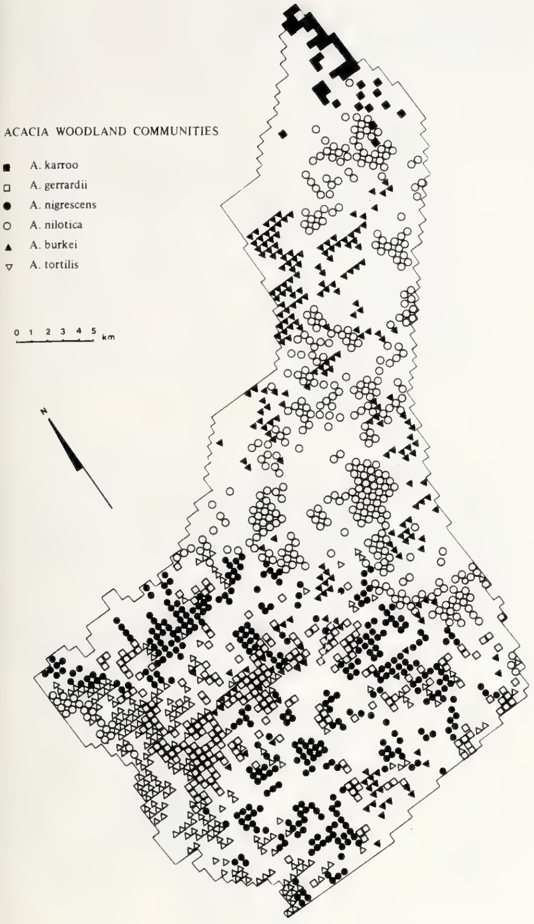

FIG. 4.—*Acacia* woodland communities.

the upper stratum and 26 species that were less than 2,0 m in height, having a frequency of less than 5% (Table 4). A dense grass sward of tall, perennial species comprises the herbaceous layer.

Acacia nilotica *Woodland*

Acacia nilotica Woodland covers extensive areas of the Corridor and Hluhluwe Game Reserve, particularly south of the Hluhluwe River (Fig. 4). It is usually found below the 300 m contour.

The dominant species characterizing this community is *Acacia nilotica,* having a frequency of 60,9% and 25,4% in the upper and lower strata (Table 3). Another 27 species were recorded for the upper tree stratum and 36 species were less than 2,0 m in height, having a frequency of less than 5% (Table 4).

In certain areas termitaria with their associated vegetation are a common feature. Widely spaced, large, emergent, often grouped, trees of *Sclerocarya birrea* subsp. *caffra* are often a characteristic feature in this woodland.

A tall, dense sward of tufted perennial grasses comprises the herbaceous layer and therefore fires are often intense.

Acacia burkei *Woodland*

Acacia burkei Woodland is found at various localities throughout the area, except for the northern part of Hluhluwe Reserve. It covers extensive areas in western Hluhluwe Reserve where it occurs on both moderately steep hillsides and flat riverine terraces in the valley bottoms. In the Umfolozi Reserve this community is usually found on broad, flat ridges at lower altitudes (Fig. 4).

Acacia burkei with a frequency of 19,0% for the upper tree stratum, was found to be dominant. The most abundant woody plant in the under stratum was *Dichrostachys cinerea,* having a frequency of 20,7% (Table 2). A total of 65 species in the upper stratum and 80 species under 2,0 m in height, were recorded having a frequency of less than 5% (Table 4).

Mainly stoloniferous grass species are present and annual species tend to be more abundant than perennials. Typically, this community grows on yellow apedal soils. These are sandy loams of the following soil series: Springfield, Cartref and Paardeberg. Where it occurs on riverine terraces, sandy soils of the Dundee form have been identified.

Acacia gerrardii *Woodland*

Acacia gerrardii Woodland (Table 5) is only found in Umfolozi Game Reserve to the south of the Black Mfolozi River, where it covers large gently undulating areas of lower and middle Ecca shales (Fig. 4).

Characteristic species of the upper stratum were found to be *Acacia gerrardii* and *A. nilotica,* having a frequency of 20,2% and 15,7% respectively (Table 3). For the under stratum *A. karroo* was the most frequent at 17,3%. Another 29 species were recorded for the upper tree stratum and 34 species were less than 2,0 m in height, having a frequency of less than 5,0% (Table 4).

A tall, rarely dense sward of mainly tufted, perennial grasses form the herbaceous layer.

Acacia nigrescens *Woodland*

Acacia nigrescens Woodland is confined to the catchment areas of the Black and White Mfolozi Rivers where it covers extensive areas throughout Umfolozi Game Reserve below the 300 m contour (Fig. 4). It is nearly always found on hillsides having a dolerite substrate.

Acacia nigrescens was found to be the dominant species characterizing the community, with a frequency of 55,0%. In the under stratum, *Acacia tortilis* with a frequency of 19,4%, was the most characteristic species (Table 3). Another 13 species were recorded for the upper tree stratum and 10 for the under stratum, having a frequency of less than 5% (Table 4).

A medium to short relatively dense sward of mixed stoloniferous and tufted perennial grasses dominate the herbaceous layer.

The community grows on margalitic soils, particularly those series of the Kiora form.

TABLE 5.—Percentage cover, canopy and ceiling heights for the different woodland communities

Woodland	Upper tree stratum mean canopy height (m)	mean ceiling height (m)	% cover	Under tree stratum mean canopy height (m)	% cover
Spirostachys africana	6,0* 9,0**	3,7	50–75	3,0	10–50
Combretum apiculatum	6,5	2,5	10–75	not discernible	
C. molle	6,3	4,0	50–75	4,0	10–25
Euclea divinorum	4,4	1,5	50–75	2,0	25–50
Acacia karroo	5,1	3,7	50–75	4,0	10–25
A. nilotica	4,1	2,6	50–80	1,5	5–10
A. burkei	8,2	6,1	50–75	5,5	10–25
A. gerrardii	3,5	1,8	20–30	1,5	5–10
A. nigrescens	8,0	3,5	25–50	1,5	5–10
A. tortilis	4,0	2,5	10–75	0,7	5–10

* Recorded in Hluhluwe Reserve.
** Recorded in Umfolozi Reserve.

Acacia tortilis *Woodland*

Acacia tortilis Woodland is confined to the catchments of the Black and White Mfolozi Rivers and occurs throughout Umfolozi Game Reserve and is usually found on east-facing hill slopes (Fig. 4).

Acacia tortilis was found to be the dominant species characterizing the community, with a frequency of 57,0% in the upper and 29,1% in the under tree strata (Table 3). Another 27 species were recorded for the upper stratum and 22 that were less than 2,0 m in height, having a frequency of less than 5% (Table 4).

A moderately short often sparse sward of tufted perennial grasses dominates the herbaceous layer.

Acacia caffra *Thicket* (3 573 ha, 3,97% of area)

Acacia caffra Thicket is found in upland situations, usually above the 300 m contour, on hillsides and ridges throughout the whole area (Fig. 5).

Characteristic species of the upper stratum were *Acacia caffra* and *Dichrostachys cinerea*, having a frequency of 46,7% and 24,2% respectively and for plants less than 2,0 m in height, frequencies were 27,0% and 20,7% respectively (Table 3). Some 31 less frequent species were found to be present (Table 4).

An average canopy height of 1,4 m was recorded for this community. However, where fire has been less frequent, plants reach approximately 3 m in height. A tall, tufted grass sward is found in association with the woody plants.

Acacia karroo – Dichrostachys cinerea *Induced Thicket* (18 504 ha, 20,56% of area)

Acacia karroo–Dichrostachys cinerea Induced Thicket is found throughout the area in steeply undulating hillsides particularly in the Corridor and Hluhluwe Reserve and may be found at all altitudes (Fig. 5).

The structure and density of this community is mainly determined by the frequency and intensity of fire. The height of woody plants varies from approximately grass height to 4,0 m, depending on the interval between burns. Typically, the spindle form of *Acacia karroo* is dominant and, when young, the tree canopies comprise few branches which increase in the absence of fire. Density of woody plants is usually very high with as many as 5 840 per hectare having been recorded.

Acacia karroo and *Dichrostachys cinerea* were found to be the dominant woody species character-

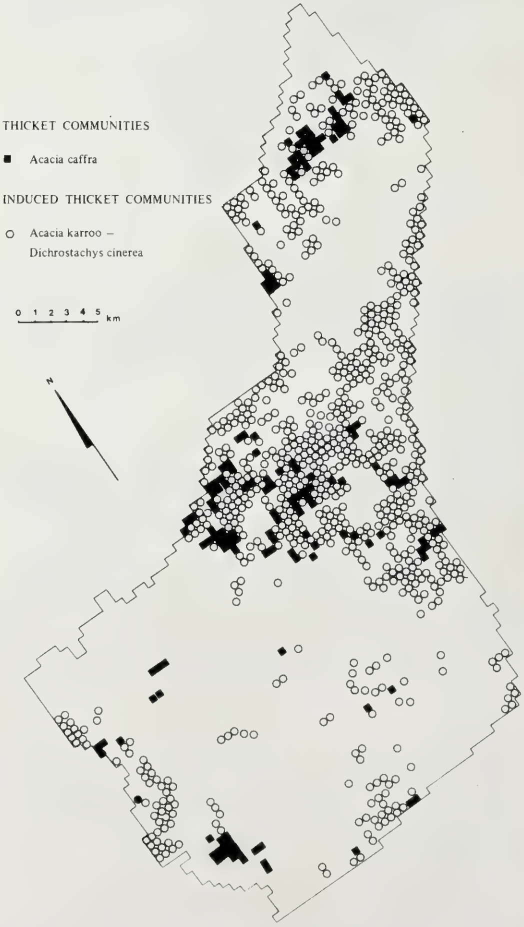
THICKET COMMUNITIES
■ Acacia caffra
INDUCED THICKET COMMUNITIES
○ Acacia karroo – Dichrostachys cinerea
0 1 2 3 4 5 km
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FIG. 5.—Thicket and induced thicket communities.

izing this community, with percentage frequencies of 44,2 and 31,0 and 17,0 and 23,5 for plants over and less than 2 m in height respectively (Table 3). Some 51 less frequent species were also recorded (Table 4).

A tall to very tall grass sward of tufted perennial species is associated with the community. This community is well utilized by both grazers and browsers and these areas constitute some of the most important feeding areas for game animals for several months following a burn. They are the most frequently burnt areas of the reserves, particularly when periods of good rains are experienced. Because of the role played by man-made fires which affect the physiognomy of this community, the term 'induced' is used to describe this thicket community.

Other communities

Few grassland areas in which woody plants are rare, are present and those that do occur, cover several hectares only. A *Themeda triandra* grassland occurs only above the 300 m contour on the top of certain high ridges and hills. A *Sporobolus africanus–Cyperus textilis* sedge-grassland is present on margalitic soils in valley bottoms in Northern Hluhluwe Reserve.

Another rare community is *Acacia davyi* Thicket which covers an area of only a few hectares at one location in Hluhluwe Game Reserve. It has an average canopy height of 1,4 m and *Acacia davyi* has a frequency of occurrence of 50,0% and 16,0% for height categories greater or less than 2,0 m respectively. Some 12 other woody plant species were found to be associated with this community.

DISCUSSION AND CONCLUSIONS

For the major species in each community (i.e. recorded frequency >5%), the ratio of plants greater than 2 m and those between 0,1 and 2 m in height was examined. In most cases, it was found that the ratio was greater than 1: 0,20. Therefore, more than 20% of the population of a particular major species were sub-canopy plants; this would indicate that possible recruitment and/or replacement of senescent canopy plants would occur at a reasonable rate. The continued existence of the community would thus be ensured. However, this was not the case with certain major species present in three woodland and two forest communities. Ratios of less than 1: 0,20 for major species were as follows:

Acacia nigrescens	1:0,7	*Acacia nigrescens* Woodland
A. grandicornuta	1:0,02	
Combretum apiculatum	1:0,02	*Combretum apiculatum* Woodland
C. molle	1:0,17	*Combretum molle* Woodland
C. kraussii	1:0,01	*Celtis africana–Harpephyllum caffrum* Forest
Celtis africana	1:0,17	
Schotia brachypetala	1:0,01	*Celtis africana–Euclea schimperii* Forest
Berchemia zeyheri	1:0,15	

Should a process of non-recruitment to the upper canopy by these plants be allowed to continue in the long term, then the physiognomy and species composition of these different communities may change radically. Such changes may possibly lead to the disappearance of the *Acacia nigrescens* and *Combretum apiculatum* Woodland communities, either completely or over wide areas in the game reserve complex. In order to establish what is limiting survival of young plants, it is suggested that autecological research be undertaken.

Species having a frequency of less than 5% are listed in Tables 2 and 4. Some of these plants are considered to be rare species. This category is defined as those woody plants that were found in either one or two communities only and have a combined frequency of less than 1%. For the forest communities 21 rare species were identified: These are:

Acokanthera oppositifolia
Albizia suluensis
Allophylus natalensis
Apodytes dimidiata
Brachylaena uniflora
Capparis sepiaria
Carissa macrocarpa
Commiphora woodii
Ficus capensis
Maerua rosmarinoides
Manilkara concolor
Nuxia floribunda
Ochna arborea
Psychotria capensis
Ptaeroxylon obliquum
Rawsonia lucida
Syzygium guineense
Trichilia emetica
Turraea obtusifolia
Urera tenax
Vangueria infausta

For the Woodland communities 24 species were similarly identified. These are:

Albizia adianthifolia
Brachylaena discolor
Bridelia micrantha
Capparis sepiaria
C. tomentosa
Carissa bispinosa
Commiphora pyracanthoides
Erythrina latissima
Euphorbia tirucalli
Ficus soldanella
Garcinia livingstonei
Grewia monticola
Iboza riparia
Kigelia africana
Maerua angolensis
M. rosmarinoides
Phyllanthus burchellii
Protea multibracteata
Rhus dentata
R. simmii
Terminalia phanerophlebia
Trema orientalis
Trichilia emetica
Vangueria infausta

It is suggested that studies into the status of these species in the Game Reserve Complex should be undertaken. Of particular concern would be the status of the endemic *Albizia suluensis* which has been listed as a threatened species (Hall *et al.*, 1980).

Some of the different plant communities found in the Game Reserve Complex have an affinity with communities in other regions of Natal. Some of these communities occur in the Tugela Basin described by Edwards (1967) and Ndumu Game Reserve described by Pooley (1977). These communities are:

Woody plant communities:

This study	*Other studies*
Acacia karroo Woodland *Acacia nilotica* Woodland *Acacia gerrardii* Woodland	Coast *Acacia karroo–Acacia nilotica–Acacia robusta* Thorn Scrub (Edwards, 1967)
Acacia karroo–Dichrostachys cinerea Induced Thicket	Coast Secondary Thicket Communities (Edwards, 1967)

Celtis africana–Harpephyllum caffrum Forest *Celtis africana–Euclea schimperii* Forest	Coast Lowland Forest (Edwards, 1967)
Combretum apiculatum Woodland	*Combretum apiculatum* Tree Veld (Edwards, 1967)
Acacia burkei Woodland *Spirostachys africana* Woodland	*Spirostachys–Acacia burkei* Woodland (Edwards, 1967)
Acacia caffra Thicket	Semi-coast Mixed *Acacia caffra* Scrub (Edwards, 1967)
Acacia tortilis Woodland	*Acacia tortilis* Woodland (Pooley, 1977)
Acacia nigrescens Woodland	*Acacia nigrescens* Woodland (Pooley, 1977)

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Vegetation survey of Sengwa

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ABSTRACT

The approach and initial results of a vegetation survey of the Sengwa Wildlife Area are outlined. The objectives were to produce a vegetation classification and map sufficiently detailed to serve as a base for the management of the natural vegetation. The methods adopted consist of (a) stratification of the area into homogeneous units using 1:10 000 colour aerial photographs; (b) plotless random sampling of each stratum by recording cover abundance on the Braun-Blaunquet scale for all woody species; and (c) analysis of the data by indicator species analysis using the computer programme 'Twinspan'.

The classification produced is successful in achieving recognizable vegetation types which tie in well with known environmental features.

RÉSUMÉ

ÉTUDE DE LA VÉGÉTATION DU SENGWA

L'ébauche et les premiers résultats d'une étude de la végétation dans la réserve de faune du Sengwa sont décrit. Les objectifs étaient d'établir une classification et une carte de la végétation suffisamment détaillées pour servir de base à la gestion de la végétation naturelle. Les méthodes adoptées consistent en (a) une stratification de la région en unités homogènes en utilisant des photographies aériennes en couleur au 1:10 000, (b) un échantillonnage au hasard de chaque strate en y relevant le coéfficient d'abondance-dominance sinvant la méthode de Braun-Blanquet, pour toutes les espèces ligneuses, et (c) l'analyse des données par l'analyse des espèces indicatrices en utilisant le programme d'ordinateur 'Twinspan'.

La classification obtenue permet de reconnaître des types de végétation qui correspondent bien au milieu étudié.

INTRODUCTION

In a developing country in which much land-use is based on exploitation of natural ecosystems there is a need for a national policy of utilization of the resources in those systems, the most basic of which is vegetation.

Planning the management of resources requires knowledge of the distribution of those resources in space; there is a need therefore, in the case of vegetation, for maps on as detailed a scale as possible. A practical approach to the mapping of vegetation necessitates classification into vegetation types. In Zimbabwe the existing vegetation classification is that of Wild & Fernandes (1967), however it is insufficiently detailed and accurate for present needs, as recognized by Robertson (1979). A useful and detailed classification would have the following features:

1. A type should represent a unique environment. This will not always be possible since communities change along environmental gradients and are not always delimited by sharp boundaries. Conversely, vegetation may sometimes be made up of a mosaic of small, well defined patches impossible to map individually. However, pragmatism dictates that divisions should be made even where it can be recognized that such a division represents an arbitrary point on a continuum, or includes more than one environment.
2. There should be a common approach by all those involved in different parts of the country, so that results are comparable.
3. The method of producing the classification should be objective. Generally, subjective methods require an ecologist with a great deal of experience. Our need is for a method that can be applied by a number of less experienced observers with the same results.

As a test-case for a rapid, detailed and objective classification, I have taken the Sengwa Wildlife Research Area (18° 10'S, 28°10'E, area 373 km^2). This area is ideal in containing a large spectrum of habitat types in a small area, and an immediate need exists for a vegetation map for research purposes.

METHODS

The methods adopted can be conveniently divided into three phases, namely stratification, description and classification.

Stratification

Ideally, one would like to sample stands at random and allow an objective classification method to construct the groups. This is inefficient because a widespread type will be oversampled, whereas a rare one may not be sampled at all, and misleading because, if a stand happens to straddle an environmental boundary, the species associations it contains will be artificial. The alternative is stratification, whereby the area is divided up into strata of similar environment and random samples are taken within strata. In the case of Sengwa, strata were identified as homogeneous patches on 1:10 000 colour aerial photographs (Figs 1 & 2). It was not expected that the strata would perfectly represent the environmental types present, i.e. some environments that had not been recognized as distinct might

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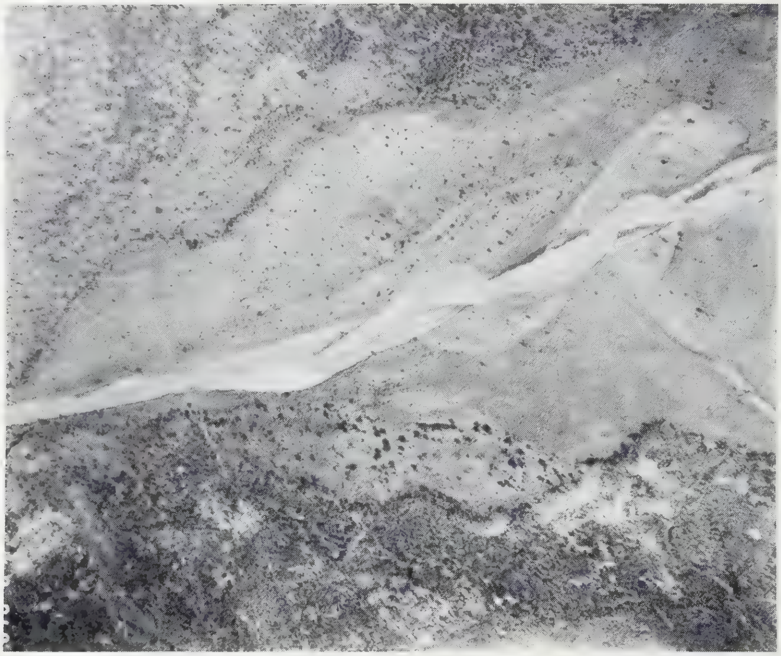

FIG. 1.—Aerial photograph of part of Sengwa Wildlife Research Area.

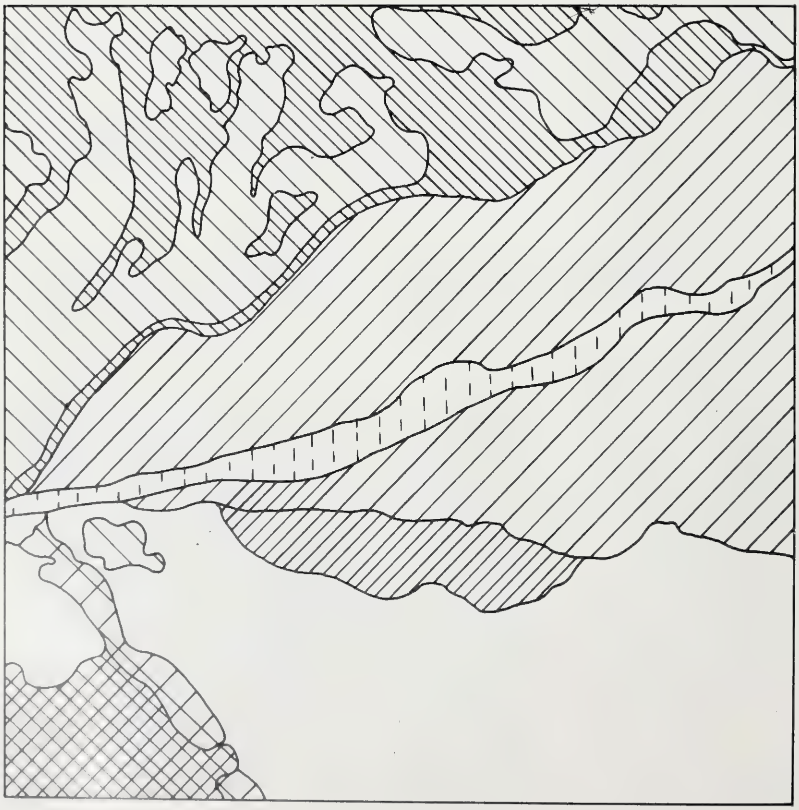

FIG. 2.—Stratified interpretation of Fig. 1.

be lumped as one stratum, leading to some undersampling. However, it is believed that the improvement over random sampling is considerable. An important constraint on strata is that they should account for the whole area. This gives all environments a good chance of being sampled whether or not they have been recognized as strata. In our case, small areas difficult to assign to strata were sampled separately. Strata which appeared more heterogeneous on the photographs were sampled more intensely. It is important to remember that the stratification represents the first hypothesis about possible types present. The subsequent classification may falsify this by making two types within one stratum. Then the hypothesis has to be refined by looking for the environmental boundary not previously seen, and resampling to test the new hypothesis. When a classification is arrived at, producing types that do not conflict with strata, there is the basis for a vegetation map. If it is not possible for the eye to detect an environmental boundary on photographs, it may still be possible to detect it by computer analysis of satellite images, though this has not been attempted at Sengwa.

Stands were chosen randomly from the strata as points from which description would begin. The presence of any stratum boundary in the vicinity was noted to guard against the generation of artificial associations.

Description

Following Robertson (1979), it was felt that woody vegetation alone could be used to characterize types. Initial trials suggested that accurate quantities give no better results than simple cover abundance. The laying out of plots was therefore deemed unnecessary. Since the size of the project requires rapid description of stands, time saved by ignoring herbs, doing no measurements and using plotless sampling was useful. Each stand was described on the basis of woody species only, the criterion for inclusion of a species being that it should be listed in Drummond (1975). From the randomly selected point, the stands were walked in a direction at right angles to the nearest stratum boundary, and away from it. Cover abundance was rated on the Braun-Blanquet scale for each species and separately for three layers, namely trees (over 3 m), shrubs (1–3 m) and small woody plants (0–1 m). (A combined estimate of these was made for later analysis.) Description was finished when no new species were seen. The main danger of having unlimited plot size is walking into a different community. This was guarded against by knowing where the stratum boundaries were, and noting whether the stand appeared homogeneous.

Classification

As an alternative to clustering methods based on generalized distance measures, I have used one based on ordination.

Ordination plots stand in multidimensional space where species are the axes. New axes are then created which express the total variation between stands more economically. When the stands are plotted on the new axes an impression of the relationship between stands is given.

Indicator species analysis (Hill, Bunce & Shaw, 1975) is a divisive method of clustering based on a reciprocal averaging ordination (Hill, 1973) which was used with some success in the classification of forest in Ghana (Hall & Swaine, 1976). This method takes the first axis of the reciprocal averaging ordination and divides the stands into two halves at the centre of the distribution. A small number of 'indicator species' are chosen according to how well their presence differentiates one side of the distribution from the other.

The groups so produced are then treated independently in the same way, thus giving a hierarchical classification. The allocation of indicators at each division enables a stand in the field to be allocated to a group using a key, and without having to consider too many species, which means once the classification has been made, a relatively inexperienced observer will be capable of placing a stand in a group in the field — a very great advantage.

With reciprocal averaging, an ordination of stands in species space and species in stand space are produced simultaneously (Hill, 1973), so the indicator analysis process can also be carried out to classify species. This enables a phytosociological table to be drawn up which displays the relation between stand groups or types an species in the classification, resembling a Braun-Blanquet association table.

The programme used for the Sengwa data was 'Twinspan' (Hill, 1979). This carries out a two-way indicator analysis for species and stands.

RESULTS AND DISCUSSION

Fig. 3 illustrates a phytosociological table constructed by 'Twinspan' on 122 preliminary stands described at Sengwa. The table is provided with stands as rows and species as columns, i.e. the reverse of the usual format. Stands have also been divided into 11 stand groups by horizontal lines. These are the groups produced by the programme, and numbering from the top, the hierarchy may be expressed as follows:

([(1 2) (3)] (4 5) (6 7)) [(8 9) (10 11)]

i.e. the first split of the analysis divided the stands in groups 1–7 from the rest, the second divided groups 1–3 from 4–7 and so on. Splits made after the third are not so meaningful in this case, though the programme could be made to carry on the process until there was one species per group.

Lines delimiting species groups have been drawn down the table; these show which species groups are important in each stand group. A black square denotes a species occurrence in a stand.

As might be expected from a divisive method such as this, when a natural group occurs in the centre of the ordination, it is likely to be split artificially. In this case, groups 8 and 3 have affinities, but have gone to different sides of the hierarchy at the first division. The groups themselves are sensible,

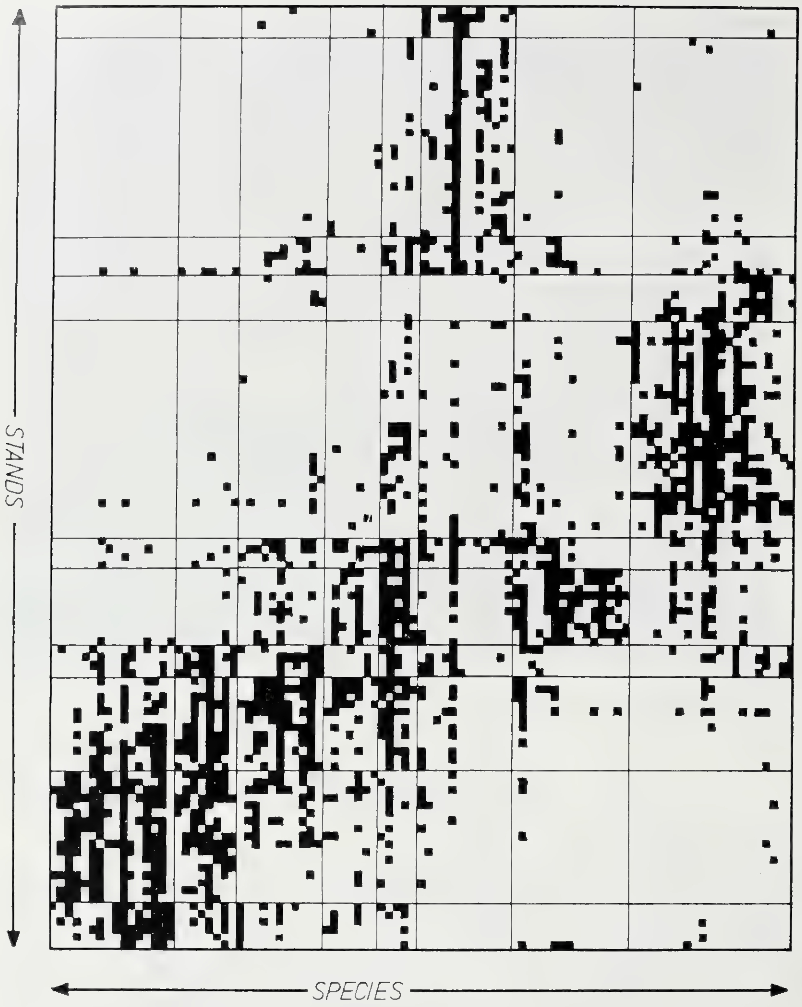

FIG. 3.—Phytosociological table 122 stands from Sengwa Wildlife Research Area constructed by 'Twinspan'.

representing different strata, but the classification is unnatural. I do not believe, however, that this detracts from its usefulness.

The classification is successful in achieving interpretable vegetation types. Working from the top, the interpretation of the 11 groups is as follows:

1. *Colophospermum mopane* woodland on calcareous soil
2. *C. mopane* woodland on clay
3. *C. mopane* woodland on shallow alluvium overlying clay.
4. *Acacia albida* flood-plain woodland.
5. *Combretum imberbe*, *C. mossambicense* river terrace woodland
6. *Combretum eleagnoides*, *Colophospermum mopane* thicket and woodland on sandy eluvium.
7. *Baikaea plurijuga*, *Combretum celastroides* dry forest and ticket on deep sands.
8. *C. mopane*, *Combretum fragrans* wooded grassland on shallow alluvium.
9. *Brachystegia* spp.– *Julbernardia globiflora* escarpment woodland on sandy soil.
10. *Brachystegia* spp.– *J. globiflora* escarpment woodland on shallow sandy soil.
11. *J. globiflora–Diplorhynchus condylocarpon* woodland and scrub on shallow gravel.

As can be seen, there is evidence of uneven sampling of environments in the table. Although it is recommended that this be avoided, the method is clearly robust where this is concerned.

Further sampling will refine the classification to the point where strata may be mapped as vegetation types.

CONCLUSIONS

The initial results of the Sengwa vegetation survey suggest that indicator species analysis on plotless stands with semi-quantitative data is a rapid and useful approach. Although initial data left something to be desired in the way of thoroughness of sampling, a good classification was produced which tied in with known environmental features.

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An ecological bibliography for southern Africa

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ABSTRACT

An ecological bibliography for southern Africa up until 1975 is currently being compiled. References recorded by researchers at the Botanical Research Institute, Pretoria are being expanded and incorporated into a computer data base. All references are annotated with codes, key words, biomes and regions where applicable. The IBM/STAIRS programme package is used for retrieving references by means of authors and subject headings as well as sorting alphabetically.

RÉSUMÉ

UNE BIBLIOGRAPHIE ÉCOLOGIQUE POUR L'AFRIQUE DU SUD.

Une bibliographie écologique pour l'Afrique du Sud jusqu'en 1975 est en cours de préparation. Les références relevées par les chercheurs à l'Institut de Recherche Botanique de Pretoria sont en train de s'accumuler et elles sont incorporées dans une base de données. Toutes les références sont annotées avec leurs codes, leurs mots clefs, les formations végétales et les régions qui les concernent. Le progiciel (produit logiciel) IBM/STAIRS est utilisé pour extraire les références sur base des noms d'auteurs et des intitulés des sujets, aussi bien que pour classer alphabétiquement.

INTRODUCTION

Because of the strong involvement of the Botanical Research Institute in plant ecological studies it was considered necessary to produce an ecological bibliography for southern Africa. By southern Africa is meant southern Africa in its broad and systematic sense, i.e. South Africa and South Tropical Africa. At the start of projects, ecologists require literature references relating to the areas which they intend studying. Usually this is time-consuming work involving much bibliographical research and reliance on the memory of the Institute's librarian. In addition to its own requirements, the Institute caters for the reference requirements of other institutions such as universities, conservation organizations and other institutes of the Department of Agriculture and Fisheries. From what has been said, it should be clear that there is a real need for an ecological bibliography.

METHODS

Since the beginning of their botanical careers the last two authors have kept and maintained fairly exhaustive card indexes to the literature of southern African ecology. The first step was to combine the two card indexes and expand them to include all possible relevant references and vegetation maps until 1975. The Universal Decimal Classification (UDC) system was used to provide a hierarchical subject classification currently consisting of approximately 200 subject headings and subheadings. Keywords, forming a lower rank where subject headings are insufficiently descriptive, are selected from each reference as they occur and form the basis of an ecological thesaurus. The key words are also arranged hierarchically in the ecological thesaurus with broad and narrow terms, synonyms and related terms indicated. Additional information such as biome, taxon number, area covered and scale where applicable, are also included with each reference.

The ecological bibliography for southern Africa will form part of the Ecology Section literature index (ESLI) data bank using the IBM System/370 computer. The IBM Storage and Information Retrieval System (STAIRS) programme package, which is available for sorting and retrieving references, will be used to sort an author index and select and sort references under various subject headings. The sorted data will then be printed by a computerized photosetting machine of the South African Documentation Centre for Agricultural Information, Department of Agriculture and Fisheries, which will provide master copies for printing.

CONCLUSIONS

The ecological bibliography for southern Africa will fulfil an urgent need by researchers for a comprehensive ecological bibliography. Considerable time will be saved at the start of projects where literature searching is often time consuming. The current expansion of references in ecology, where other disciplines are often involved, makes a computerized data bank for literature essential. Loading of the data into the data bank is at an advanced stage and test runs for retrieval, sorting and printing have been conducted. Publication of the ecological bibliography for southern Africa as a Botanical Survey Memoir is envisaged for 1982, whereupon loading of data for the period 1976–1982 will commence.

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Acacia tortilis subsp. *heteracantha* productivity in the Tugela Dry Valley Bushveld: preliminary results

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ABSTRACT

Acacia tortilis Hayne subsp. *heteracantha* (Burch.) Brenan dominates secondary succession in the Tugela Dry Valley Bushveld of the Natal midlands. The parts of KwaZulu in this veld type are impoverished, overpopulated and over-grazed. Preliminary results indicate that at a density of 2 700 ± 600 trees/ha there is a standing crop of c.2,87 t/ha (DM) of acacia twigs suitable for hand pruning and milling into fodder, but that this is a costly process. Herbage biomass peaked at 0,73 t/ha (DM). Veld condition assessments suggested a stocking rate of 0,1 AU/ha (grazers), but actual grazer stocking rates may be many times this density. It is recommended that the browser/grazer ratio be altered to make use of the c. 1,05 t/ha (DM) of shoot growth produced annually by *A. tortilis* subsp. *heteracantha*.

RÉSUMÉ

*LA PRODUCTIVITÉ DE L'*ACACIA TORTILIS *SUBSP.* HÉTÉRACANTHA *DANS LE BUSHVELD DE LA VALLÉE SÈCHE DE LA TUGELA: RESULTATS PRÉLIMINAIRES*

L'Acacia tortilis *Hayne subsp.* heteracantha *(Burch.) Brenan, domine dans la succession secondaire dans le bushveld de la valée sèche de la Tugela dans les Midlands au Natal. Les zones du KwaZulu dans ce type de veld sont appauvries par la surpopulation et le pâturage intensif. Des résultats préliminaires indiquent qu'à une densité de 2 700 ± 600 arbres/ha, il y a une récolte sur pied de c. 2,87 t/ha matière sèche de rameaux d'acacia susceptibles d'être taillés manuellement et broyés en fourrage, mais ceci est un procédé coûteux. La bio-masse d'herbage a son optimum à 0,73 t/ha. Des estimations du rendement du veld ont suggéré une densité de cheptel de 1 animal broutant par 10 ha, alors que les densités du cheptel paîssant actuellement peuvent être largement supérieures. Il est recommandé que le rapport broutage des rameaux/broutage de l'herbe soit modifié afin d'utiliser les c. 1,05 t/ha de jeunes rameaux produits annuellement par* A. tortilis *subsp.* heteracantha.

INTRODUCTION

This paper presents preliminary findings of a study of the productivity of *Acacia tortilis* Hayne subsp. *heteracantha* (Burch.) Brenan relative to that of the herbage at contrasting sites in secondary acacia veld in Bioclimatic Zone 10 of Natal (Phillips, 1967). The aim of the study is to assess the carrying capacity of the veld for browsers and grazers in order to maximize production and minimize environmental degradation.

Study species

Acacia tortilis (Forsk.) Hayne, a flat-topped thorn tree with indehiscent, coiled pods, is widely distributed in the drier parts of Africa — from the northern Cape and Natal to Arabia (Ross, 1975). Subspecies *heteracantha* (Burch.) Brenan, the subject of this study, occurs throughout the interior of Natal and indeed throughout most of southern Africa. Its basionym is *A. heteracantha* Burch., and synonyms are *A. litakunensis* Burch., *A. spirocarpoides* Engl. and *A. maras* Engl.

Study area

All data presented in this study were collected on a farm on the Weenen-Msinga border (Fig. 1), 26 km upstream from Tugela Ferry, but the study will be extended to other areas of *A. tortilis* subsp. *heteracantha* semi-deciduous bush, where this occurs as a secondary community in Tugela Dry Valley Bushveld (Edwards, 1967).

This type of vegetation falls within Bioclimatic Group 10 (Phillips, 1973), which Thorrington-Smith *et al.*, (1978) describe as having low agricultural potential, and as being overstocked, denuded and eroded, with spectacular bush encroachment. The topography is broken with many stoney hills. Temperatures are extreme with frost in winter and a mean daily summer maximum of 30°C. Rainfall is low (637 mm), unreliable, and generally accompanied by electric storms (Edwards, 1967; West, 1950).

The population density of Bioclimatic Zone 10 of KwaZulu is given as 50 people/km^2 (Thorrington-Smith *et al.*, 1978), but hut counts suggest that it may be higher (Schulze, 1969). Topographic factors and resettlement schemes have resulted in areas of locally high population density, and the environmental degradation in the vicinity of these is severe and is characterized by vegetation destruction, dongas and drying up of springs. As Thorrington-Smith *et al.* (1978) point out, cultivation without irrigation is hazardous, so much of the money and food required is brought in from the cities or irrigated white farms, thereby artificially boosting the carrying capacity. Livestock, particularly cattle, are cherished as insurance to be sold in times of dire need or to be sacrificed on special occasions. Tribal land is common land exploited by all to provide fuel, grazing and building materials, but where carrying capacity has been exceeded the "system of the commons is absolutely intolerable" and the environment is degraded, further reducing carrying capacity (Hardin, 1977).

Secondary acacia communities are the product of ploughing, over grazing or other forms of disturbance (Edwards, 1967; West, 1950). Under heavy

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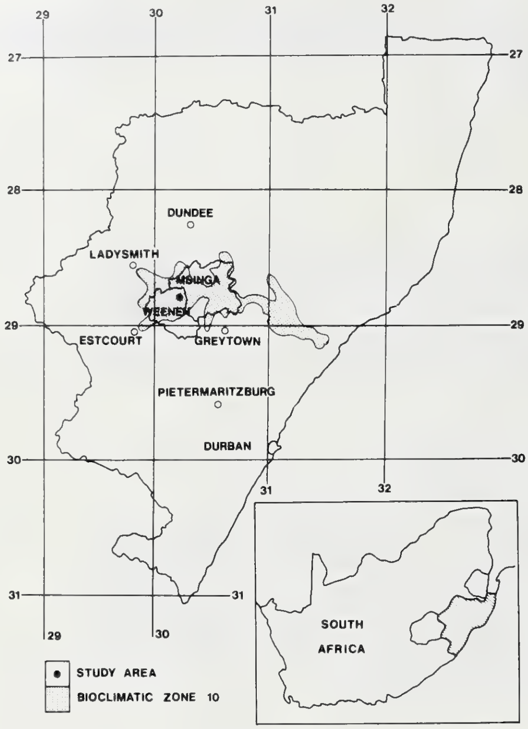

FIG. 1.—Study area in relation to the Weenen and Msinga Districts, and the distribution of Bioclimatic Zone 10 in the Tugela Valley. Inset: South Africa, Natal Province shaded.

grazing such bush lands deteriorate rapidly and become more woody or eroded (Kelly & Walker, 1976; Whyte, 1947). Removal of thorn trees would be not only costly and difficult to implement, but would deprive local people of ‘free’ fuel and fencing. As browse appears to be under-utilized and herbage over-utilized in semi-arid rangelands (Whyte, 1947; Trollope, 1975; Kelly, 1977) it may be cheaper, more acceptable and more productive to alter the grazer-browser ratio.

METHODS

Density, biomass and production of A. tortilis *subsp.* heteracantha

Density was estimated from stem and tree (stems joined on or below ground level) counts on 80 10 × 10 m plots distributed over five sites. Stem diameter, referred to as basal diameter in this paper, was measured approximately 20 cm above soil level. To estimate the standing crop of biomass available for milling into fodder, trees were pruned with long handled shears, and the shorn shoots (approximately 1 cm diam.) of individual trees at sites 2, 4, 5, 6 and whole plots at sites 1 & 3 were weighed in the field using a spring balance. Two methods were used to estimate annual production. Firstly, all the new season's twigs were measured, counted and clipped from 9 trees of known diameter, then weighed. Secondly, 10 new season's twigs from each of 10 trees were measured. The number of twigs per branch approximately 2,2 cm diam. was recorded, as was the number of such branches per tree of known diameter. Total twig mass was estimated from total length. This method was also used when comparing the growth of pruned and unpruned trees, and of trees of different ages.

The pod crops of 64 measured trees were weighed in the field, and podbearing trees counted in two quarter hectare quadrats. To obtain diameter-mass regressions, 68 trees were felled at site 6. Diameters were measured and prunable twigs and wood weighed separately in the field. The leaf dry mass/pruned branch fresh mass ratio from site 1 was used to provide a rough estimate of dry leaf yield per unit area. Leaf production and retention data are based on counts of leaves on the terminal 10 cm of new seasons shoots.

Herbage composition, utilization, cover and biomass

Species composition at two sites was assessed using the step-point method (Mentis, in press) and data obtained were used to estimate veld condition (Tainton *et al.*, 1980) and utilization ratios for each species:

utilization ratio = % use / % occurrence

where use is evidence of grazing. Cover at these sites was measured at two monthly intervals using a 100 point grid half a metre square. Ten 1/4 m^2 plots per 1/4 ha quadrat were then clipped, oven dried and weighed to obtain a grid number/mass relationship. The grid was also used when comparing herbage cover beneath acacia canopies with that in the open. At site 6 where shrubby forbs prevented the use of the grid, a perforated horizontal bar was used to assess cover.

RESULTS AND DISCUSSION

Acacia density, prunable biomass and production

Tree densities are similar to those of *A. karroo* Hayne in the Valley Bushveld of the Eastern Cape (Aucamp, 1976) and semi-arid mopane in Zimbabwe (Kelly & Walker, 1976). 4,56−6,84 t/ha (FM) of branches suitable for milling into bush ‘hay’, are available for hand pruning (Table 1. At site 6, where canopies would have been out of reach, 16,6 t/ha of such branches were harvested when the trees were felled. The relationship between basal diameter and harvestable shoot fresh mass was as follows:- log

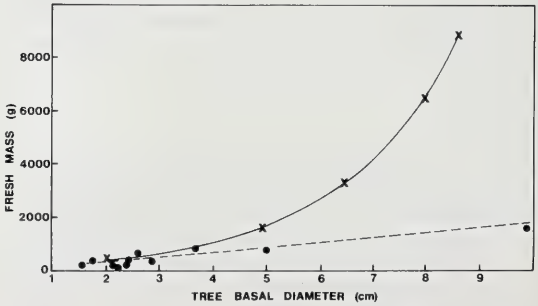

FIG. 2.—Tree diameters related to pruning biomass and annual shoot production: —×—, pruning yield at Site 6 (g FM) relative to diameter (cm) log mass −2,24 + 0,17 diameter; r − 0,845; n−68; - -●- -, annual shoot production of individual trees (g FM), curve fitted by eye.

TABLE 1.—Harvestable *Acacia* biomass and shoot production

Site description no & appearance	Stem diam. cm	Tree density no/ha	Prune biomass kg/ha(FM)	Production * kg/ha/yr(FM)
1 dense, 1 m regen.	2,0(0,1)	4428(703)	4896(672)	2670 −1328
2 dense, 1,5 m	2,9(0,1)	2533(149)	6844(609)	2507
3 open, 1−2,5 m	4,0(0,4)	1460(300)	4560(930)	1368−876
4 thicket, 2 m	5,1(0,3)	2416(217)	6547 −	1933
5 as above	5,4(1,8)	"	5798 −	2114
6 closed, 3 m	6,6(0,3)	1667(312)	16576(3251)	3889

* Rough estimate based on mass derived from eye fitted curve (Fig 2) and stem density (not shown).

mass (g) = 2,42 + 0,17 basal diam. (cm); r = 0,848; n = 55 (Fig. 2).

Assuming a 50% moisture content, the rough estimate of annual shoot production (Table 1) is comparable with that of semi-arid Mopane-veld: 594−2 121 kg/ha/yr DM (Kelly & Walker, 1976) and central African savanna: 1 500 kg/ha/yr DM (Trollope, 1981)., however, it is low when compared to the 5 000 kg/ha/yr available to giraffe in the mixed *Acacia* veld of Serengetti (Felker, 1981).

The effects of pruning, size-class and species on shoot growth

Pruned trees tended to produce longer and more branched shoots with greater diameters than unpruned trees, and this trend was more marked under heavy pruning than under light pruning (Table 2). The most dramatic differences were in mean shoot length at Site 1 ($F_{1,46} = 8, 6$; $P = 0{,}01$), and in stem diameter at Site 3 ($F_{1,23} = 9{,}2$; $p = 0{,}01$). As fewer shoots were produced by pruned trees, the total shoot length per branch c. 2,2 cm diam. was only marginally greater in pruned than in unpruned trees ($F_{1,22} = 2{,}9$; $P = 0{,}2$).

Young trees (2,1−2,9 cm diam.) at Site 1 produced longer, plumper and more highly branched shoots than did the older trees (4,9−5,3 cm diam.) at Site 3. The difference in lateral shoot number was most significant: ($F_{1,64} = 9{,}9$: $P = 0{,}01$). *A. karroo* reacted to pruning in the same way as *A. tortilis* subsp. *heteracantha* but produced shorter, less branched shoots than the latter (Table 2). The difference in lateral shoot number between the two species was greater under heavy pruning ($F_{1,55} = 12{,}4$: $P = 0{,}01$).

Site 1 yielded 62,8 (19,4)% of the initial prune mass when repruned 10 months later. Heavily pruned plots at Site 3 yielded 20,5 (0,5)%, and lightly pruned plots 11,8 (0,2)% of the original harvest mass at the second prune. These data suggest that the smaller diameter classes have a more rapid recovery rate.

Leaf production and loss

During the summer the density of leaves on new seasons twigs is 1,84 (0,1) leaves/cm. Production of leaves is not significantly affected by pruning, but leaf retention during winter is influenced by site

TABLE 2.—Pruning, size-class and species effects on shoot growth

Acacia tortilis subsp. *heteracantha*	Treatments; mean (SEM)*				
Plot Pruning intensity	3 control	3 light	3 heavy	1 light	1 heavy
Tree diameter (cm)	*5,0(0,4)*	*4,9(0,3)*	*5,3(0,4)*	*2,9(0,2)*	*2,1(0,1)*
mean shoot length (cm)	24(3)	48(6)	71(4)	88(19)	130(20)
no. laterals/shoot	0,6(0,2)	1,9(0,3)	2,6(0.8)	5,4(0.9)	10.1(0.6)
shoot diameter (cm)	0,4(0,01)	*0,5(0,02)*	*0,5(0,03)*	*0,6(0,01)*	*0,7(0,05)*
no. shoots/branch	*33(7)*	*30(1)*	24(4)	--	--
shoot length/branch (cm)	860(30)	*1480(24)*	*1730(250)*	--	--
Acacia karroo					
mean shoot length (cm)	--	--	--	*61(11)*	*73(9)*
no. laterals/shoot	--	--	--	2,2(0.6)	3.6(0.3)

*Pairs of results which do not differ significantly are italicized.

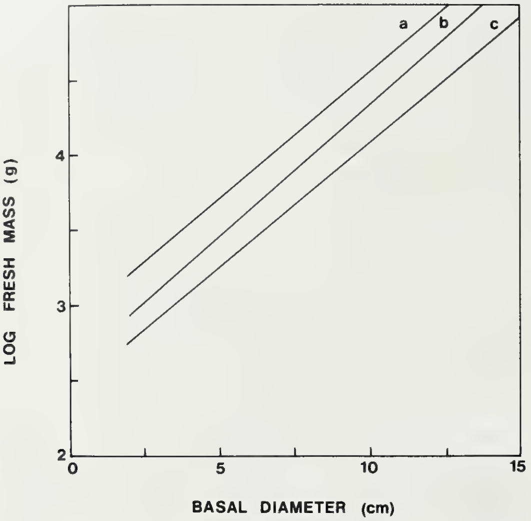

FIG. 3.—Basal diameter (cm)-fresh mass (g) relationships (Site 6): a, total biomass — n = 54, r = 0,891, log y = 2,85 + 0,17 x; b, wood mass — n = 57, r = 0,899, log y = 2,56 + 0,18 x; c, pruned shoots — n = 55, r = 0,845, log y = 2,42 + 0,17 x.

($F_{3,347}$ = 11,7; P = 0,001), pruning ($F_{1,238}$ = 6,8; P = 0,01), and among pruned trees, by tree diameter class ($F_{2,117}$ = 4,4: P = 0,05).

Soil moisture during the dry season appears to be the major site factor affecting leaf retention. In July, leaf retention of trees growing on the banks of the Tugela was c. 71% of the summer density at this site, 20 m above the Tugela 57% of the leaves were retained, 200 m above the Tugela on old fields, 30% and on very shallow soils at this altitude, 10% *A. tortilis* subsp. *heteracantha* trees are often leafless on higher, drier ground during the winter, and it is possible that frost also affects leaf attention.

The ratio of pruned branch fresh mass to air-dry leaf mass was 1: 0,052. Sites 1–5 would therefore yield 237–355 kg/ha air dry leaves.

Basal diameter/mass relationships and size-class distribution

An old *A. tortilis* subsp. *heteracantha* stand with a closed canopy had a wood crop of 23,2 (5,9) t/ha (FM) as compared with the 58–76 t/ha (FM) wood crop of 12 year old *A. tortilis* subsp. *heteracantha* trees of a north African subspecies growing in plantations in India (Muthana & Arora, 1980).

Weed, pruneable branch and total tree fresh mass increase logarithmically on basal diameter (Fig. 3). The wood yield of a self-established acacia stand should be estimated from the sum of the products of mass and frequency for each size class, and not from mean tree diameter as neither frequency nor mass are normally distributed in the size classes (Fig. 4). This also applies to branch and total biomass, as it is not uncommon for c. 25% of the trees to constitute c. 75% of the biomass.

During the period August 1980–August 1981 there was no significant change in the circumferences of a sample of 92 old stems marked at Site 6. The young trees at Site 1, however, showed a mean diameter increment of 0,58 (0,17) cm, a change significant at the 1% level.

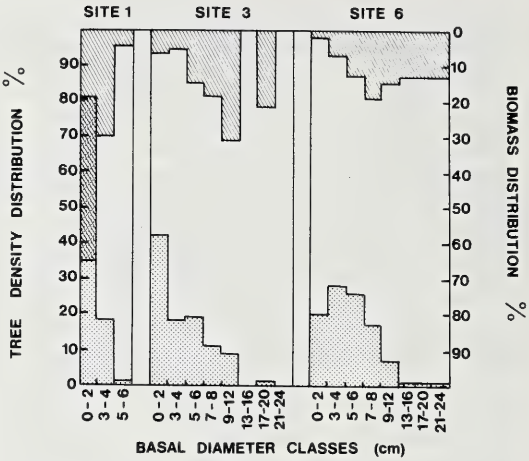

FIG. 4.—Tree density and biomass distribution in basal diameter classes.

A. tortilis subsp. *heteracantha* at Site 3 starts to bear pods when in the 6–8 cm diameter class. Pod yield then increases exponentially on diameter (Fig. 5), but possibly falls off steeply in very old trees. c. 30 cm diam. Stunted trees on very shallow shaley soils started to bear in the 2–4 cm diam. class, and yield increased linearly on basal diameter. At site 3

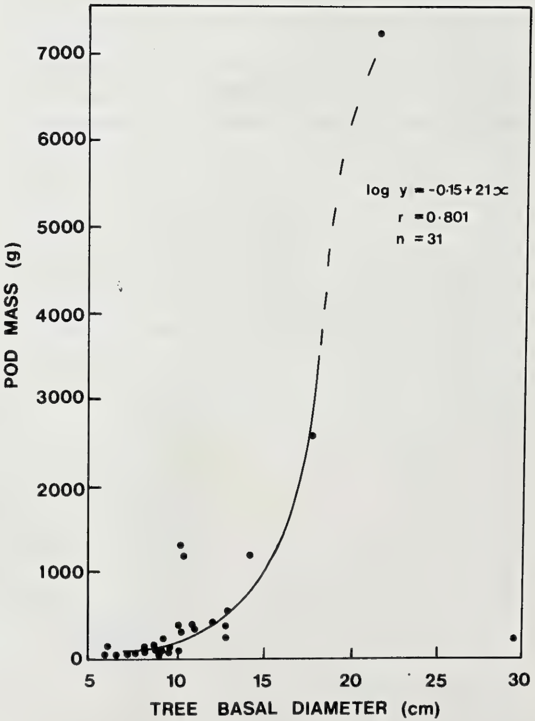

FIG. 5.—Relationship between pod yield (g) and basal diameter (cm) at Site 3. Note: the largest tree is excluded from the regression calculation.

TABLE 3.—Nutritional value and cost of acacia fodder

Product *Acacia tortilis* subsp. *heteracantha*	% Protein	% Fibre	% Fat	Cost c/kg	Cattle preference
Milled shoots average	*6,9(0,6)*	*47,0(1,2)*	*1,43(0,26)*	7–10	2
Milled leafy shoots	8,2	43,8	2,15		
Milled bare shoots	4,9	49,9	1,01		
Milled pods	15,2(1,1)	24,3(1,7)	1,81(0,10)	22–27	1
Dry green leaves	14,4(0,1)	19,6(0,9)	5,70(0,79)	30–70	3
Other feeds					
Eragrostis hay	6,0	44,5	2,0	8	
Lucerne hay	17,1	35,1	2,0		
Dairy meal					

where fruiting trees had a mean basal diameter of 11,2 (0,8) cm, the mean yield was 0,73 (0,25) kg/tree, and the maximum yield was 7,2 kg/tree. Pod yields recorded in the study area range from 1–139 kg/ha: very low compared with the 10–12 kg/tree in *A. tortilis* plantations in India (Muthana & Arora, 1980) or the 250–500 kg/ha yield of pods in natural stands in Zimbabwe (West, 1950).

Nutritional value, processing costs, and sundry uses of acacia products

The nutritional value of acacia fodders is acceptable, however, they are not cheap (Table 3). Costs shown include labour, fuel and maintenance of the machinery, but not the capital costs. Dry green leaves were obtained by stacking branches until they were dry, then beating off the leaves. A similar method is used for harvesting *Leucaena* leaves in Australia (Wildin, 1980) and would have been ideal for poor rural areas had not the thorns been shed with the leaves making the product unacceptable to cattle. Cattle, goats and horses accept milled branches and pods, and cattle have been maintained for up to two years on these products at the C.A.O. co-op farm at Weenen. Goats will eat 300–500 g pod meal per day in addition to browsing, and the meal may also be used as a poultry feed.

In the Msinga District, *Acacia tortilis* subsp. *heteracantha*, although not a preferred fuel wood, is much used for cooking and heating; the bark is used to tie bundles and roof laths, and the branches to construct thorn fences around kraals and gardens. These fences, which are renewed every year or two, comprise large branches packed together at a density of about 6,7 branches/m to form a breast high barrier. Three gardens sampled in Nomoya were enclosed by 65 (5) m of thorn fence comprising some 400 branches c. 4 cm diam. or the equivalent of 0,2 ha of bushes- an area ten times as great as that of a garden.

Herbage biomass, condition and response to acacia cover

Biomass on heavily grazed oldlands (Sites 3 & 7) peaked in January at 830 (139) and 630 (76) kg/ha DM. Although $\frac{2}{3}$ of the grass at site 7 died between mid January and mid March, protein content dropped only slightly from 10,5% in February to 9,9% in April. The April protein content of *Bothriochloa*-dominated Site 3 was 5,1%. Fibre content of the herbage at both sites was low (25,9%) probably because the grasses, being continually grazed produced few inflorescences.

A veld condition assessment (Table 4) showed that all three study plots were overgrazed relative to the Bioclimatic Zone 10 benchmark. They also contained shade tolerant and old land species not found in the benchmark. Although the protein content and the species composition score of Site 3 is lower than that of Site 7, the former site is dominated by selected or neutral species, and the latter by avoided species.

Under a closed acacia canopy perennial forbs dominate, but the summer foliage cover (43%) is similar to that of open sites (37–40%). Where acacias are scattered, grass cover is higher under their canopies (18,7%) than between the canopies (8,8%) during winter ($F_{1,24}$ = 12,9; P–0,01). Grass under thorn trees is probably less accessible to grazers.

CONCLUSION

A standing crop of 5,7 t/ha FM (c. 2,9 t/ha DM) of acacia branches was available for hay making in secondary *A. tortilis* subsp. *heteracantha* veld, however, milling woody plants is an expensive way of maintaining an artificially high grazer population. The annual production of acacia shoots, 2,1 t/ha FM (c. 1,1 t/ha DM) was greater than the herbage biomass peak of 0,7 t/ha. The veld should therefore be stocked with as many or more browsers than grazers (within the limits of carrying capacity). Whereas it may be difficult to convince some people of the merits of increasing the browser/grazer ratio, because of social and cultural attitudes to cattle (ARDRI, 1981), this should be less disruptive and costly than an attempt to remove the trees and establish pasture for beef production — the solution implied by Thorrington-Smith *et al.*, (1980). It may

TABLE 4.—Veld condition

	Benchmark Zone 10*	Site 3	Site 7	Site 6
Acacia density (trees/ha)	121	1460	1300	1972
Canopy cover	open	open	open	closed
Taxa	*Themeda triandra*	*Bothriochloa insculpta*	*Urochloa mosambicensis*	Perennial forbs
% & utilization †	60 --	43 1,2	24 0,8	35 --
	Sehima galpinii	*Urochloa mosambicensis*	*Tragus berteron.*	*Panicum* sp.
	14 --	27 0,9	21 0,7	28 --
	Panicum spp.	*Aristida* spp.	Annual forbs	*Sporobolus smutsii*
	7 --	8 1,0	14 0,7	21 --
Composition score	100	8	14	30
% decreasers	89	4	13	30
% increaser II	7	66	30	21
% spp not in benchmark	--	30	57	49
Current grazing capacity AU/ha	0,2	0,11	0,10	0,14

* Data provided in Tainton *et al.* (1980).

† Utilization: see methods.

be feasible to camp and rest common land, but this is also likely to be complicated and costly.

'No specific studies have been undertaken on the growth of key browse species' (Trollope, 1981), and the value of leguminous trees for soil improvement, fuel and fodder has only recently been acknowledged (Folker, 1981). Although, as Janzen (1973) points out, they are not the solution to land management problems, we cannot afford to get rid of them before we have investigated their potential.

ACKNOWLEDGEMENTS

The Church Agricultural Co-op Farm Committee stimulated my interest in *A. tortilis* subsp. *heteracantha* productivity and this preliminary study was based on the farm. I am most grateful to Prof. J. Hanks for making available to me the facilities at the Institute of Natural Resources, University of Natal and for assisting in many other ways, and also to Prof. N. Tainton and Mr M. Mentis for their advice. The preliminary research was financed by B.P. (South Africa).

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Etat actuel des recherches sur la flore et la végétation du Rwanda et du Burundi

M. REEKMANS* et G. TROUPIN**

RÉSUMÉ

Dès la fin du siècle dernier, de nombreux explorateurs, surtout allemands, ont parcouru le Burundi à la recherche des fameuses sources du Nil et des légendaires 'Monts de la Lune'. Outre des descriptions souvent précises des paysages botaniques rencontrés, on leur doit de nombreuses récoltes, mais dont une grande partie, hélas, a disparu avec les bombardements de Berlin en 1944–1945.

Avec 1919 et le passage du Burundi sous tutelle de la Belgique, les botanistes de ce pays ont assuré la relève et réalisé d'assez nombreuses récoltes dans le pays. Les expéditions étaient organisées à partir du Zaïre et le plus souvent de courte durée; c'est ainsi que jusqu'en 1965 il n'y eut pas d'exploration systématique du pays, ce que traduisait le rapport de l'AETFAT en 1964 en classant la Burundi parmi les régions mal connues d'Afrique.

Cette exploration systématique du pays débuta en 1965 avec J. Lewalle. Outre la publication d'un excellent travail sur l'étagement de la végétation, on lui doit la récolte de plus de 6 500 numéros d'herbier, dont plusieurs espèces nouvelles. Il travailla au Burundi jusqu'en 1972.

De 1970 à 1980. M. Reekmans a récolté au Burundi plus de 9 500 numéros d'herbier, surtout dans les secteurs peu explorés auparavant. Il a publié plusieurs travaux relatifs à la phénologie des espèces et aux associations végétales du Burundi occidental.

Répondant aux invitations de Lewalle et de Reekmans, de nombreux botanistes ont eu l'occasion de parcourir le pays et d'y faire des récoltes dans des domaines très particuliers.

Actuellement, on peut dire qu'à l'exception d'un tout petit secteur du pays, (par ailleurs bien connu du Rwanda où il a fait l'object de plusieurs études), la flore du Burundi est bien connue. Les limites des influences phytogéographiques y sont bien précisées et la publication d'une carte de la végétation est prévue pour bientôt. Un catalogue de la flore du pays est aussi en voie de réalisation.

Outre ces résultats 'scientifiques,' les travaux de botanique au Burundi ont aussi eu pour effet de sensibiliser les autorités du pays à la 'valeur' de leur patrimoine naturel, au point qu'en mars 1980, un Institut National pour la Conservation de la Nature a été créé. Sa première mission sera de délimiter et d'assurer la création de parcs nationaux et de plusieurs réserves naturelles qui permettront la sauvegarde de quelques espèces très intéressantes.

ABSTRACT

THE PRESENT STATE OF RESEARCH ON THE FLORA AND VEGETATION OF RWANDA AND BURUNDI

At the end of the last century, many explorers, mainly Germans, travelled in Burundi searching for the famous sources of the Nile and the legendary 'Mountains of the Moon.' Apart from the very often accurate descriptions of the vegetation and flora they encountered, one is indebted to them for the rich harvest of specimens collected, many of which were destroyed in the bombing of Berlin in 1944–1945.

When, in 1919, Burundi was placed under Belgian mandate, Belgian botanists took over the work and collected numerous specimens in the country. Their expeditions were organized from Zaïre and were often of short duration, with the result that in 1965 there was still no systematic exploration of the country and in 1964 AETFAT classified Burundi as one of the lesser known areas in Africa.

Systematic exploration of the country began in 1965 with J. Lewalle. Apart from the publication of an excellent work on the stratification of the vegetation, he collected more than 6 500 numbers of herbarium specimens, several of which represented new species. He worked in Burundi until 1972.

From 1970 to 1980, Reekmans collected more than 9 500 specimens for the herbarium, mainly in the areas that were not intensively explored previously. He has published several works in connection with the phenology of species and vegetation association of western Burundi.

Many botanists invited by Lewalle and Reekmans, have had the opportunity to explore the country and to collect specimens of special groups.

At present, it can be said that, except for a very small area of the country (otherwise well known in Rwanda where several studies have been made) the flora of Burundi is now well known. Phytogeographical limits are well established and the publication of a vegetation map is due in the near future. A catalogue of the country's flora is also to be published shortly.

Apart from these 'scientific' results, botanical studies in Burundi have also had the result of awakening the authorities to the 'value' of their natural heritage — to such an extent that in March 1980 a National Institute of Nature Conservation was created. Its first aim will be to ensure the establishment of natural parks and several natural reserves in which some very interesting species will be preserved.

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Situés aux confins de la région guinéo-congolaise, coincés entre les domaines oriental et zambésien de la région soudano-zambésienne et intégrés par leurs parties les plus élevées à la région afromontagnarde, le Rwanda et le Burundi offrent des végétations très variées et une grande richesse floristique. Les influences orientale et montagnarde (jusqu'à un étage afro-alpin dans la chaîne des Birunga) sont toutefois plus marquées au Rwanda qu'au Burundi, où, par contre, l'élément zambésien est nettement mieux représenté.

Si au Rwanda, surtout à la faveur de la création des parcs nationaux de l'Akagera et des Birunga, la flore et la végétation font l'objet de nombreuses études depuis plusieurs décennies, il n'en est pas de même au Burundi, où jusqu'en 1965, les travaux en la matière furent plutôt rares: seuls en fait quelques secteurs très limités en extension avaient fait l'objet de prospections botaniques et d'études phytosiologiques. L'AETFAT concrétisait d'ailleurs cette situation en 1965, en classant le Burundi parmi les pays d'Afrique à flore méconnue, voire inconnue.

A l'occasion d'assemblées pléniéres antérieures de l'AETFAT, notamment en 1970 à Munich, des rapports détaillés concernant les travaux floristiques réalisés au Rwanda et au Burundi ont déjá été présentés. Nous limiterons donc notre mise au point à une synthése des recherches effectuées depuis cette date.

LE RWANDA

Phanérogames et ptéridophytes

Exploration et missions botaniques

De 1969 à 1972, G. Bouxin et M. Radoux, séjournant dans le pays dans le cadre d'une mission patronnée par l'Institut National de Recherche Scientifique du Rwanda (INRS), se sont consacrés principalement à la prospection du Parc National de l'Akagera et de la forêt de montagne de Nyungwe-Rugege, c'est-à-dire des régions les moins altérées du pays. Cette campagne, à laquelle participèrent également P. Bamps, B. Runyinya, G. Troupin et O. Ubonabenshi se solda par la récolte d'environ 4 000 numéros d'herbier. Parallèlement et surtout à partir de 1971, l'intérêt s'est déplacé vers les secteurs moins connus du pays et vers les volcans qui n'avaient plus été prospectés depuis 30 ans. C'est grâce à l'appui du Fonds de la Recherche Fondamentale Collective de Belgique (FRFC) que furent organisées deux missions de 3 mois qui visitèrent notamment la chaîne des Birunga et les forêts de montagne. Elles devaient se dérouler de décembre 1971 à mars 1972 et de juillet à octobre 1974 et regroupaient surtout des botanistes belges: P. Auquier, J. L. de Sloover, J. Lambinon, J. Rammeloo, G. Troupin et P. van der Veken. Ces missions ont permis la récolte de plus de 5 000 numéros d'herbier ainsi que de nombreuses graines pour distribution et études caryologiques.

De 1971 à 1978, d'autres campagnes de récoltes furent encore organisées par l'INRS. (G. Troupin, B. Runyinya) et axées essentiellement sur la prospection des endroits les moins visités antérieurement.

Du 5 au 30 juin 1978, à l'initiative de l'Université Nationale du Rwanda à Butare, l'Agence de Coopération Culturelle et Technique (ACCT) mit sur pied, à travers le pays, une expédition ethnobotanique visant à accélérer la réalisation de l'inventaire floristique du pays et à favoriser la mise en valeur du patrimoine naturel par le développement de techniques adaptées au monde rural. En fait, elle voulait ainsi assurer l'épanouissement des recherches relatives à la pharmacopée et à la médecine traditionnelle.

Regroupant des spécialistes de disciplines diverses — médecine, pharmacie, chimie, botanique (en particulier, feu J. Raynal, du Muséum d'Histoire Naturelle de Paris) — elle a permis, sur le plan strictement botanique, la récolte de 1 062 numéros d'herbier, correspondant à 699 taxons.

G. Troupin a fait plusieurs séjours au Rwanda en 1980 et en 1981. En 1980, D. Bridson et lui-même se sont plus particulièrement intéressés à trois familles importantes: Acanthaceae, Lamiaceae et Rubiaceae. A cette occasion aussi, G. Troupin a récolté dans la forêt de montagne de nombreux échantillons de bois destinés au Service des Bois du Musée de Tervuren.

Parmi les apports d'herbiers, figurent aussi les transferts à Butare (1972 & 1973) de quelque 4 000 spécimens récoltés au Rwanda entre 1956 et 1963 et qui avaient été déposés à l'herbarium de l'IRSAC à Lwiro (Zaïre).

Au total, si on tient compte de toutes les activités botaniques réalisées au Rwanda depuis le début du siècle, on peut estimer qu'on dipose actuellement de ± 25 000 numéros d'herbier de plantes vasculaires déposés au Jardin Botanique National de Belgique à Meise et pro parte à Butare, Kew, Nairobi, Liège, Gand et Paris.

Etudes de la flore et de la végétation

En 1971, G. Troupin publie son 'Syllabus de la Flore du Rwanda, Spermatophytes.' Il y présente une analyse succincte des familles représentées, avec une caractérisation de genres exemplatifs. En 1975, en collaboration avec N. Girardin, il réalise une clé pratique de détermination des plantes ligneuses du Parc National de l'Akagera et des savanes orientales du Rwanda.

La richesse de la flore forestière du pays, de la forêt naturelle de Nyungwe en particulier (400 à 500 espèces ligneuses), apparaît au travers des publications du Projet Pilote Forestier de Kibuye (PPF) de la Coopération suisse et notamment du guide des principales essences de la forêt de montagne du Rwanda de J. Combe (1977).

Le premier volume de la 'Flore du Rwanda, Spermatophytes', est sorti de presse en 1978. G. Troupin (avec la collaboration de plusieurs spécialistes) y traite 62 familles et 421 taxons de rang spécifique et infraspécifique. Le deuxième volume est en voie d'achèvement et sa parution attendue pour 1982. Pour le volume III, 16 familles (dont les

Rubiaceae) ont été traitées et pour le volume, IV, le manuscrit de 4 familles est déjà rédigé.

Dans le même contexte, depuis 1970, la Flore d'Afrique Centrale, a publié 31 fascicules, traitant de familles présentes au Rwanda.

D'autres documents floristiques importants sont actuellement sous presse. C'est notamment le cas de la 'Flore des plantes ligneuses du Rwanda' de G. Troupin. Cette flore, due à l'initiative du PPF de Kibuye et réalisée avec la collaboration de D. Bridson, traite de tous les arbres, arbustes, buissons et lianes reconnus dans le pays, y comprises les essences étrangères subspontanées ou en voie de naturalisation. Y figurent: 726 espèces, réparties en 336 genres et 98 familles ainsi qu'une abondante illustration couvrant 85% de la flore.

L'ensemble des travaux floristiques réalisés depuis 1970 a permis de reconnaitre parmi les récoltes plus de 350 taxons nouveaux pour la flore du Rwanda, pays cependant signalé comme bien connu par l'AETFAT en 1965.

Les Ptéridophytes sont également en cours d'étude par R.Pichi-Sermolli, qui devrait bientôt faire une synthèse de la flore ptéridologique du Rwanda et du Burundi.

Dans les domaines de la phytogéographie, de la phytosociologie et de la pharmacologie, on trouve en outre pendant la période 1971–1981, des publications de chercheurs de l'INRS et de l'Université Nationale du Rwanda à Butare et notamment de: L. Angenot, G. Bouxin, J. P. Chapelle, M. Radoux, B. Runyinya et L. van Puyvelde. En cytotaxonomie, nous citerons surtout des travaux de P. Auquier et R. Renard.

Herbarium national du Rwanda (INRS Butare)

Les spécimens d'herbier récoltés au Rwanda avant 1968 avaient été dispersés dans les herbariums voisins, notamment à Yangambi et Lwiro (Zaïre), à Nairobi, à Kew, à Rubona et à Bruxelles, au point qu'à cette date, l'herbarium de Butare ne comportait qu'un millier de numéros provenant essentiellement des récoltes de Troupin.

La récupération des collections rwandaises de Lwiro et de Rubona (6 500 numéros) et les apports des nombreuses campagnes de récolte organisées dans le pays entre 1969 et 1976 (10 000 numéros) ont permis la constitution d'un herbarium qui, après élimination des récoltes abîmées ou insuffisantes et des duplicata superflus, regroupe approximativement 15 000 numéros d'herbier dignes de conservation.

Cryptogames

De très nombreuses récoltes de cryptogames, notamment de champignons, de lichens, de mousses et d'hépatiques ont été réalisées, surtout à l'occasion des deux missions du Fonds de la Recherche Fondamentale Collective. D'autres matériaux ont été recueillis plus occasionnellement par J. Lambinon à l'occasion d'un passage au Rwanda en 1980. Des études systématiques et de répartition phytogéographique de ce matériel sont actuellement en cours et plusieurs publications sont sorties de presse. Nous signalerons à ce propos les travaux de J. L. de Sloover et C. van den Berghen (mousses et hépatiques) de J. Lambinon et E. Sérusiaux (lichens), ainsi que de J. Rammeloo, de V. Demoulin et D. M. Dring et de L. Ryvarden (champignons).

LE BURUNDI

Phanérogames et ptéridophytes

Exploration et missions botaniques

Comme nous l'avons signalé précédemment, les travaux botaniques et les récoltes au Burundi furent plutôt rares jusqu'en 1965. A l'époque, seuls le Mosso (G. Michel & J. Reed) et le bassin de la Karuzi (D. van der Ben) et dans une certaine mesure aussi la plaine de la Rusizi, prospectée par R. Germain surtout sur sa rive zaïroise, pouvaient être considérés comme relativement bien connus. Cette situation résulte, semble-t-il, du fait que le Burundi ne disposait ni de parc national, ni de réserves naturelles dignes de ce nom, susceptibles d'attirer les chercheurs, ainsi que de l'état de dégradation apparent de sa couverture végétale.

Ce n'est donc qu'à partir de 1965 que des prospections systématiques et des récoltes abondantes furent réalisées à l'initiative de J. Lewalle. Pendant son séjour au Burundi (de 1965 à 1972), celui-ci a rassemblé plus de 6 500 numéros d'herbier et accueilli plusieurs missions étrangères, ce qui a permis de développer les récoltes au niveau des bryophytes (E. Petit) et des ptéridophytes (R. Pichi-Sermolli). Les herbiers de Lewalle comportent surtout des spermatophytes et des ptéridophytes, mais aussi des échantillons de bois pour études anatomiques (Tervuren) et bon nombre d'hépatiques épiphylles.

C'est de la même époque que datent les récoltes d'orchidées de N. Delarge et de phaséolées de J. C. Baudet.

De 1970 à 1981, M. Reekmans a récolté au Burundi plus de 10 700 numéros d'herbiers. De nombreux doubles ont été largement distribués et figurent actuellement dans les collections de Meise, de Nairobi, du Missouri Botanical Garden, de Kew, de Liège, de Gand et de la Vrije Universiteit te Brussel.' Les collections Reekmans comportent surtout des plantes vasculaires, et accessoirement des bryophytes, des mycètes et des lichens épiphytes ou épiphylles. On y trouve aussi de nombreux échantillons de bois pour étude anatomique, de diaspores pour les collections de Meise et de graines ou de matériel vivant pour celles de l'Université de Liège.

Les récoltes de J. Lewalle et de M. Reekmans furent à l'origine d'une prise de conscience de l'intérêt encore évident de la flore du Burundi. C'est ainsi que la mission du Fonds de Recherche Fondamentale Collective (FRFC) séjourna aussi au Burundi pendant plus d'un mois (septembre-octobre 1974) et y récolta, outre plusieurs milliers de spécimens d'herbier de phanérogames et de cryptogames, quantité de diaspores et graines pour étude cytotaxonomique.

Pendant leur séjour au Burundi, G. Guigonis et C. Pouilloux, de la Mission Forestière Française pour la Crête-Zaïre-Nil (MFFCZN) récoltèrent aussi un certain nombre de numéros d'herbier de plantes ligneuses des forêts et galeries forestières.

A l'occasion de missions plus occasionnelles, R. Bouharmont, J. Lambinon, C. Renard et J. J. Symoens ont rassemblé de nombreux matériaux supplémentaires.

Depuis trois ans, dans le cadre de la préparation d'un doctorat en sciences botaniques, P. Ndabeneze a recueilli plus de 1 000 numéros de graminées sur le territoire du Burundi et, depuis quelques mois, A. Caljon a entrepris à son tour la réalisation d'un herbier; ses récoltes se poursuivent actuellement.

Etudes de la flore et de la végétation

Avant 1977, on ne disposait en matière de flore et de végétation du Burundi, que des seuls travaux de R. Germain (plaine de la Rusizi), de G. Michel et J. Reed (Mosso) et de D. van der Ben (bassin de la Karuzi). Depuis lors, plusieurs publications importantes sont apparues.

J. Lewalle a publié les résultats de ses observations sur les étages de végétation au Burundi occidental (1972) puis sur l'endémisme dans la remarquable vallée de la Syguvyaye (1976).

Récemment (1980–1981), sont sortis de presse des articles de M. Reekmans relatifs à la flore de l'Imbo et à sa phénologie, aux associations végétales de la plaine de la Rusizi, à la phytosociologie et à l'importance phytogéographique des forêts à *Julbernardia* du Burundi.

D'autres travaux concernant la phénologie des associations végétales de la plaine de la Rusizi, ainsi que la situation actuelle et les perspectives en matière de conservation de la nature au Burundi sont actuellement sous presse. J. Lambinon et M. Reekmans ont également publié une note concernant l'intérêt de la flore du Burundi en général, et de certains biotopes plus particuliers, en prônant la mise sur pied, dans le triangle Kivu-Rwanda-Burundi, d'un tourisme culturel qui serait rapidement profitable aux trois pays.

L'importance, l'intérêt et la variété de la flore du Burundi apparaissent aussi à travers les nombreuses citations de spécimens dans les fascicules de la Flore d'Afrique Centrale (surtout depuis 1970).

Un essai de synthèse des données phytogéographiques et phytosociologiques relatives au Burundi a été tenté par C. Pouilloux, sous forme d'une carte du tapis végétal publiée dans le récent 'Atlas du Burundi' (1979). Malgré ses imprécisions et certaines erreurs, cette carte constitue un document de base intéressant.

Des essais de réalisation de clés pratiques de détermination des arbres et des arbustes de certains secteurs du Burundi ont été tentés par J. Lewalle, M. Reekmans et J. Lambinon. Actuellement, ces outils, dont le Burundi a le plus grand besoin, sont au stade de l'expérimentation et de l'évaluation et n'ont donc encore reçu qu'une diffusion très limitée. Leur mise au point définitive et leur publication devraient être effectives prochainement.

Il convient également de souligner le nombre relativement important d'espèces nouvelles décrites récemment à partir des récoltes du Burundi. C'est là un témoignage de l'intérêt de sa flore et de l'originalité des végétations de certains de ses secteurs.

Sur le plan paléobotanique, il faut encore signaler la découverte (puis la description anatomique) de troncs pétrifiés dans la plaine de la Haute-Rusizi. Les résultats de ces études font l'objet d'une communication dans le présent 'Proceedings.'

Herbarium

En fait, le Burundi ne dispose pas encore d'un 'herbarium' digne de ce nom et la plupart des récoltes se trouvent dispersées à l'étranger. Il faut toutefois signaler que des doubles des récoltes récentes — notamment de la mission FRFC, de J. Lambinon et de M. Reekmans — ont eté déposés au Département de Botanique de l'Université du Burundi, où ils sont accessibles.

Cryptogames

D'importantes collections de champignons ont été réalisées par J. Rammeloo au cours de l'expédition du FRFC de 1974; elles furent complétées à l'occasion d'une mission de plus longue durée organisée en 1979, à l'initiative du Jardin Botanique National de Belgique. J. Lambinon a aussi collecté surtout des Gastéromycètes et des Aphyllophorales. Le dépouillement et la publication des résultats est en voie de réalisation. Dans ce même domaine, il faut également signaler les récoltes de F. Dossin effectuées dans diverses parties du Burundi entre 1974 et 1978.

Dans le domaine des lichens, il faut noter les importantes collections rassemblées par J. Lambinon à l'occasion de ses divers séjours au Burundi (1974–1975–1978–1980) et accessoirement celles de M. Reekmans (surtout épiphylles). Une étude de ce matériel est actuellement en cours à l'Université de Liège et plusieurs notes (Sérusiaux-Lambinon) sont déjà sorties de presse.

Outre les récoltes de E. Petit (1967), des collections de mousses et d'hépatiques ont été réalisées par J. L. de Sloover à l'occasion de la visite de la mission FRFC au Burundi (1974). Elles ont donné lieu, avec les récoltes du Rwanda et du Kivu (Zaïre), à la publication de plusieurs notes importantes. Occasionnellement, J. Lewalle et M. Reekmans ont également participé à la collecte de mousses et d'hépatiques (surtout épiphylles).

PERSPECTIVES

Si au Rwanda, à la faveur de l'existence de parcs nationaux et de réserves naturelles, la flore et les végétations les plus caractéristiques du pays ne paraissent pas directement menacées, du moins à court terme, il n'en est hélas pas de même au Burundi. Ici, malgré les cris d'alarme lancés depuis des années, les formations naturelles cèdent de plus en plus à la poussée démographique inquiétante. Il faut toutefois signaler, qu'au vu des résultats récents obtenus surtout en botanique, il a été créé au Burundi (1980) un Institut National pour la Conservation de la Nature (INCN) qui, à travers la protection de quelques biotopes remarquables et éventuellement leur mise en valeur sur le plan touristique, vise aussi à la sauvegarde de leurs espèces les plus intéressantes.

Bothalia 14, 3 & 4: 779–784 (1983)

The vegetation of the Cape of Good Hope Nature Reserve

H. C. TAYLOR*

ABSTRACT

The Cape of Good Hope Nature Reserve, 7 750 ha in extent, occupies the southern end of the Cape Peninsula. Geologically, it is composed of sandstone beds of the Table Mountain Group of the Cape Supergroup. Topographically, it comprises an interior plateau bounded partly by hills and mountains which reach 360 m on the False Bay coast.

Two structural formations, fynbos and broadleaved scrub, are recognized. Within fynbos, the two floristic categories, Inland and Coast Fynbos, reflect the two major soil types present. The flora of the Reserve, with 1 060 species (35% monocots, 65% dicots) comprises 40% of the flora of the Cape Peninsula. About 40 species are either endemic or rare and endangered to varying degrees.

Alien woody plants that have invaded the veld over the past half-century are presenting a serious and costly management problem.

RÉSUMÉ

LA VÉGÉTATION DE LA RÉSERVE NATURELLE DU CAP DE BONNE ESPÉRANCE

La Réserve naturelle du Cap de Bonne Espérance, d'une superficie de 7 750 ha, occupe l'extrémité méridionale de la péninsule du Cap. Géologiquement, elle est composée de gisements de grès du groupe de la montagne de la Table dans le Super-Groupe du Cap. Topographiquement, elle comprend un plateau intérieur bordé partiellement par des collines et des montagnes atteignant 360m sur le côte de False Bay.

Deux formations structurales, le fynbos et la formation broussailleuse à grandes feuilles, sont reconnues. Dans le fynbos, les deux catégories floristiques, le Fynbos Côtier et le Fynbos de l'Intérieur, réflètent les deux principaux types de sols présents. La flore de la Réserve, avec 1 060 espèces (35% de monocotylédones, 65% de dicotylédones) comprend 40% de la flore de la péninsule du Cap. Environ 40 espèces sont soit endémiques, soit rares, et menacées à des degrés divers.

Des plantes ligneuses étrangères qui ont envahi le veld au cours du dernier demi-siècle présentent un sérieux et coûteux problème de contrôle.

ENVIRONMENT

The Cape of Good Hope Nature Reserve, 7 750 ha in extent, occupies the southern end of the Cape Peninsula which is the most south-westerly point of the African continent. Bounded on the west by the cold Atlantic Ocean and on the east by the warmer waters of False Bay, no point on the Reserve is further than 5 km from the coast and the influence of the sea is everywhere felt. The whole Reserve is composed of level or gently inclined sandstone beds of the Table Mountain Group of the Cape Supergroup, resting on Cape granite which is visible only at the base of the Cape Point cliffs. Block-shaped boulders formed by joint and bedding-plane weathering, are typical of this formation (Figs 1 & 2). The diagonal land boundary of the Reserve follows the line of a fault. The chain of hills south of the fault valley merges into the mountain range of the False Bay coast, with summits to 360 m. The eastern slopes of these mountains, truncated by wave attack, drop almost sheer to the sea, but the western slopes fall less steeply to a central plateau (Figs 3 & 4) that shelves westward for 5 to 6 km until it is terminated in a sandstone scarp (Fig. 1). The present coastal shelf may extend up to half a kilometre westward of the scarp, but is usually narrower (Figs 2 & 5). Inland dunes, now stabilized, occur in the southern part of the Reserve. The soils derived from the Table Mountain Group sandstones are acid, whereas those developed on marine sand dunes are usually neutral or alkaline.

The Mediterranean-type climate is unusually cool and equable for this latitude (34°S). It is tempered in summer by strong south-east winds, often with cloud, whereas in winter the boisterous north-westerly gales bring cool, moist air off the Atlantic, resulting sometimes in days of stormy rain. Rainfall averages 700 mm per annum near the mountains, but the Cape Point rain-gauge records less than half this amount. The gradual transition between summer and winter gives rise to prolonged spring and autumn seasons. The west coast is often clothed in fog during autumn.

Although the Southern Cape Peninsula had been inhabited by primitive man from the earliest Stone Age, it was only after the Dutch East India Company developed Simon's Bay as a winter anchorage in 1742, that the ecosystem became conspicuously altered, initially by destruction of the natural game, later by the practice of stock farming with attendant frequent burning and overgrazing. As large-scale commercial agriculture developed in the hinterland, the smallholdings of the southern Peninsula became uneconomic. Between 1938 and 1965 the area was acquired by the Divisional Council of the Cape as a Nature Reserve. The Divisional Council aims eventually to re-establish the natural

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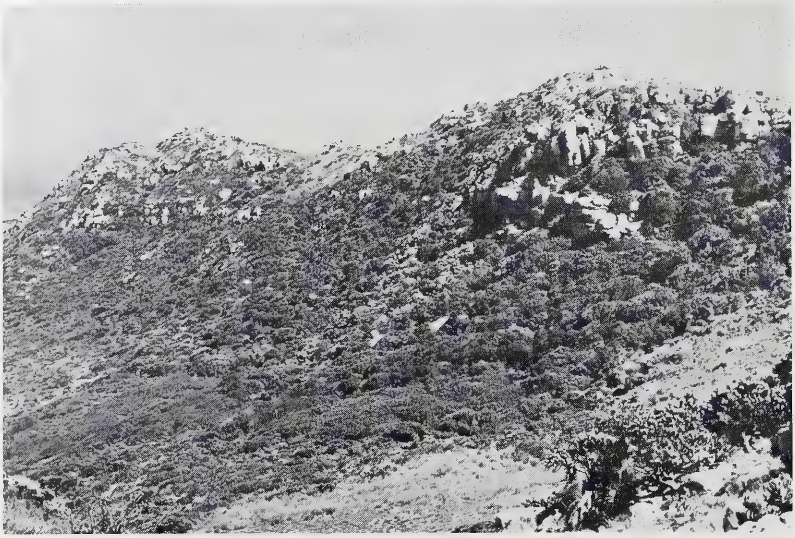

FIG. 1.—Broad-leaved Scrub at Gifkommetjie. Tall Scrub on scree slopes with *Tarchonanthus camphoratus* (grey) and *Maurocenia frangularia* (dark green). Below it and to left, *Sideroxylon* Scrub on old dunes. Foreground coastal Dune Fynbos.

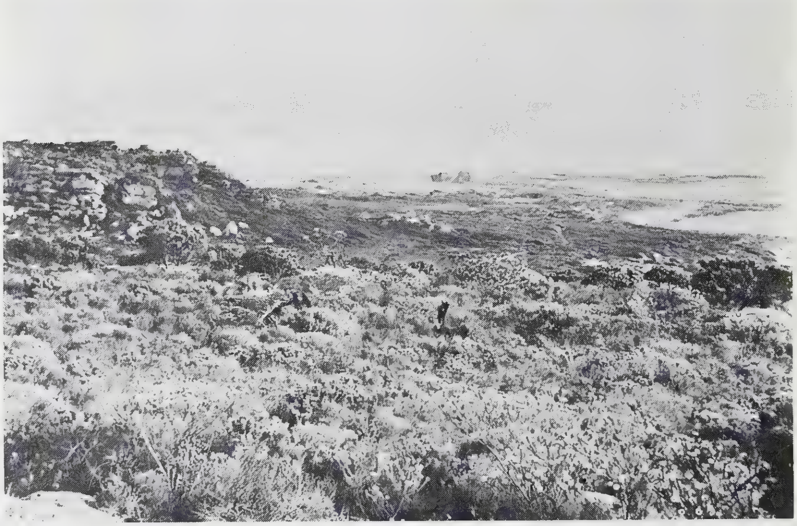

FIG. 2.—Western Hillveld variety of Upland Mixed Fynbos near Olifantsbos with the endemic white-flowered *Staavia dodii* in the foreground and the scattered 2-m high proteoid shrub *Leucospermum conocarpodendron* beyond. Remains of the Thomas Tucker, wrecked in 1941, on the distant shore.

conditions prevailing at the time of the early settlers, while catering for the recreational needs of an increasing number of visitors.

VEGETATION

In 1966 and 1967 the author carried out trials of vegetation survey methods on the Cape of Good Hope Nature Reserve and, as a result, the Braun-Blanquet phytosociological method has been widely adopted for primary surveys of South African vegetation including fynbos (Taylor, 1969 and in preparation).

Two structural formations, fynbos and broad-leaved scrub, may be recognized on the Reserve. Fynbos occurs on sites exposed to fire, whereas scrub develops fully only in certain habitats where fire is excluded.

Fynbos, the shrubby, heath- or maquis-like

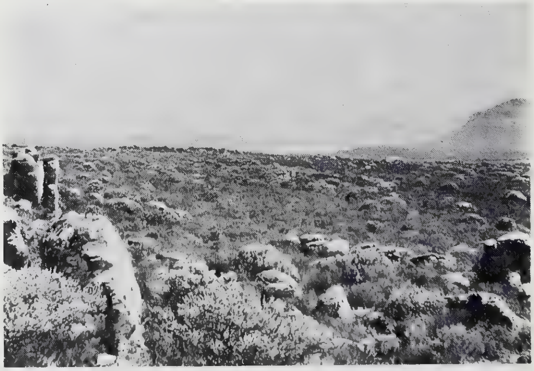

FIG. 3.—Restionaceous Plateau Fynbos, about 13 years post-burn, with typical three-layered vegetation. Scattered, domed, light green shrubs are *Leucadendron laureolum* c. 1,5 m; middle layer dominated by *Salaxis flexuosa*. In foreground among rocks, *Aspalathus capensis* (rigid green shrub) and *Erica mammosa* (white flowers).

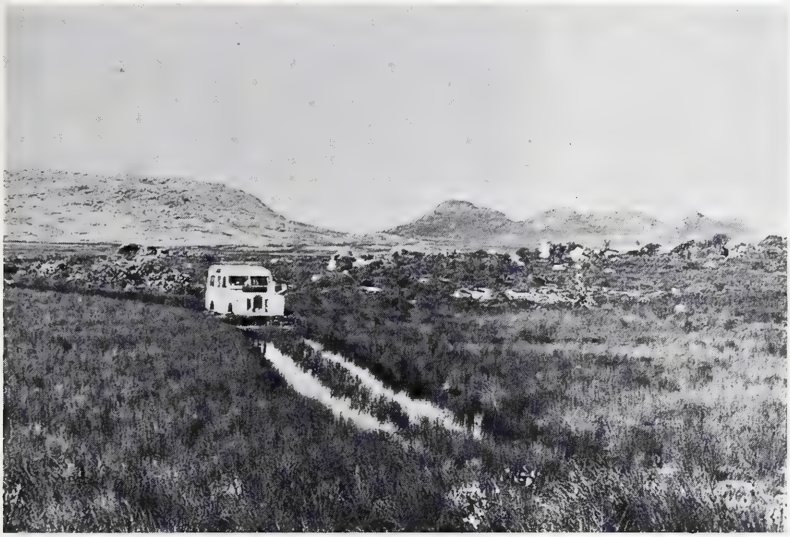

FIG. 4.—Poorly drained parts of the plateau become temporary pans in winter. Restionaceous Tussock Marsh with *Elegia parviflora* dominant on lower right, near Sirkelsvlei.

vegetation typical of the southern and south-western Cape Province (Taylor, 1978), occupies about 97% of the area of the Reserve. It has three distinctive physiognomic elements, restioid, ericoid and proteoid (Taylor, 1977). The two floristic categories, Inland and Coast Fynbos, reflect the two major soil types present. The most complete structural development is seen in the Inland Fynbos of the better-drained, slightly sloping parts of the plateau (Fig. 3) where the vegetation is three-layered with a discontinuous upper stratum of the proteoid *Leucadendron laureolum,* a middle stratum, about 50–90 cm high, of wiry ericoid or narrow-sclerophyll shrubs among which the families Asteraceae, Ericaceae, Rutaceae, Thymelaeaceae and Rosaceae *(Cliffortia)* are conspicuous, and a lower stratum of tufted, wiry hemicryptophytes, mainly Restionaceae (e.g. *Thamnochortus dichotomus*) and Cyperaceae. On poorly drained parts of the plateau where bedrock lies close to the surface, both upper and middle strata are absent and the Restionaceae of the lower stratum strongly dominant (*Elegia parviflora* in Fig. 4). Communities of the rocky hills are floristically the richest, the ericoid middle layer being well developed and the proteoids scattered (*Leucospermum conocarpodendron* in Fig. 2), though in the early post-fire stages the resprouting hemicryptophytes, including grasses, dominate.

Coast Fynbos of the alkaline dune soils, comprising a different suite of species, is similar to Inland Fynbos in structure but lower in stature (Fig. 1, right foreground) and the proteoid element (usually *Leucadendron coniferum)* only becomes conspicuous in the more sheltered slacks and depressions. Rocky coasts, where the Table Mountain Sandstones are exposed, have skeletal soils that are acid like the inland hill soils but, unlike the latter, are close to base saturation. Many of the shrubs are ericoid or narrow-sclerophyll, fleshy or succulent, low, sprawling or cushion-shaped, pruned or scorched by the salty winds off the sea. In rocky places, broad-sclerophylls of the scrub intrude (Fig. 5).

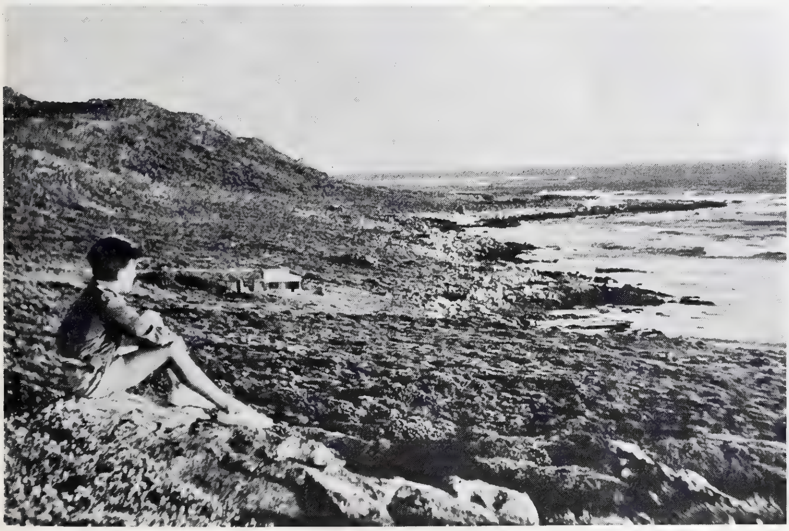

FIG. 5.—Fynbos developing to Broad-leaved Scrub at Ribboksdam. 'Taylor's Shack' was demolished in 1968.

The broad-leaved scrub, a simplified form of the coast forest of the Knysna region, is floristically distinct from fynbos. On dune sands it forms thickets, 2–4 m high, of sprouting broad-leaved sclerophylls dominated by *Euclea racemosa* and *Sideroxylon inerme* (Fig. 1, left foreground), but on rocky screes of the western escarpment which are better protected from fire, it develops into a gnarled mixed scrub of dwarf forest with a canopy height up to 5 m (Fig. 1, right) where *Pterocelastrus tricuspidatus, Tarchonanthus camphoratus, Maurocenia frangularia* and *Chionanthus foveolatus* are among the principal tree species.

FLORA

The present check list of the flora of the Reserve, with 1 060 species (35% monocots, 65% dicots) comprises 40% of the flora of the Cape Peninsula (Adamson & Salter 1950). The eleven most important families, in descending order of species richness, are Asteraceae, Cyperaceae, Fabaceae, Iridaceae, Orchidaceae, Ericaceae, Restionaceae and Poaceae (tied), Liliceae, Campanulaceae and Proteaceae.

About 40 species, including 10 of Erica, are either endemic or rare and endangered to varying degrees. Four examples represent the different categories of noteworthy species. *Watsonia tabularis* (Fig. 6) is endemic to the Cape Peninsula but widespread in the Reserve and not endangered. By contrast, *Leucadendron macowanii* (Fig. 7) is endemic to the

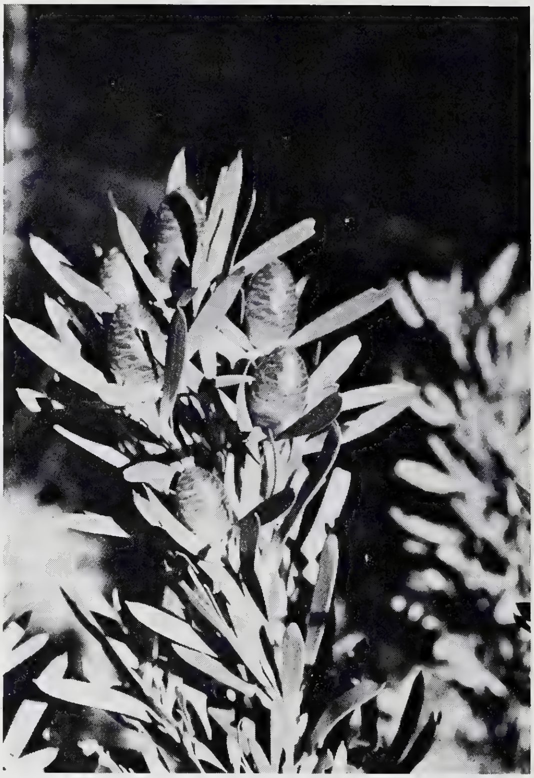
Fig. 7.—*Leucadendron macowanii*, endemic to the Reserve, with a severely restricted distribution, seriously endangered.

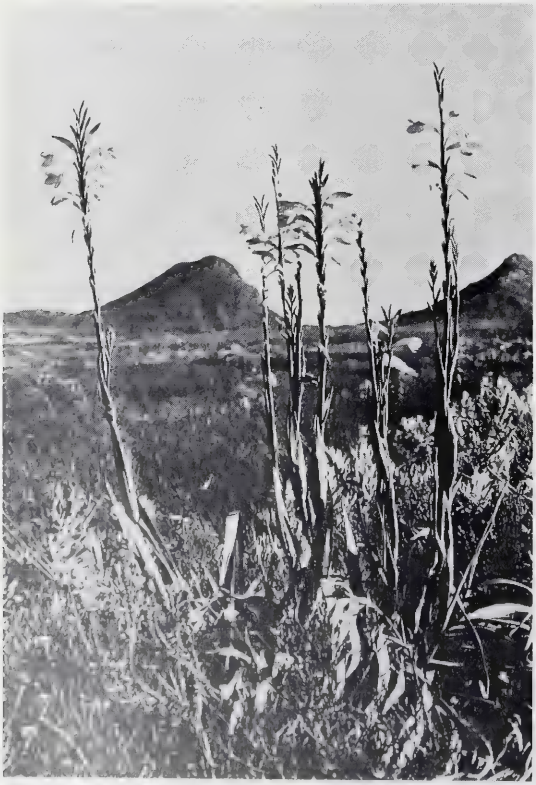
Fig. 6.—*Watsonia tabularis* var. *concolor*, endemic to the Cape Peninsula, but not threatened.

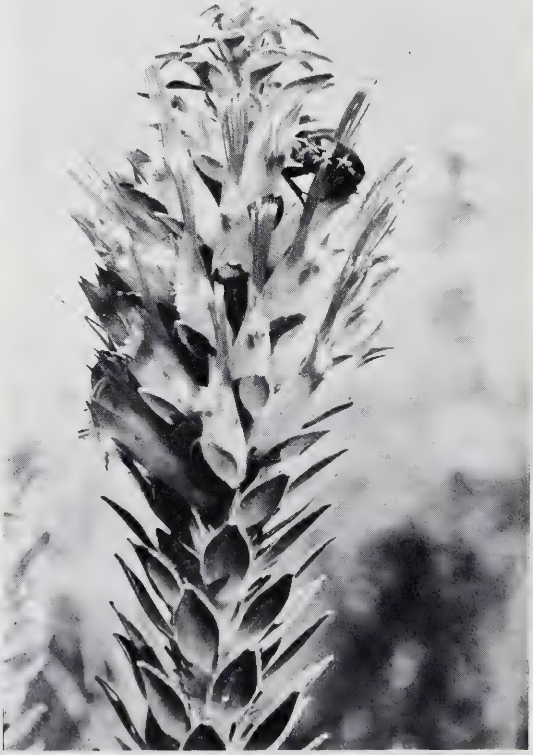
Fig. 8.—*Mimetes hirtus*, uncommon on the Reserve, but neither endemic nor threatened.

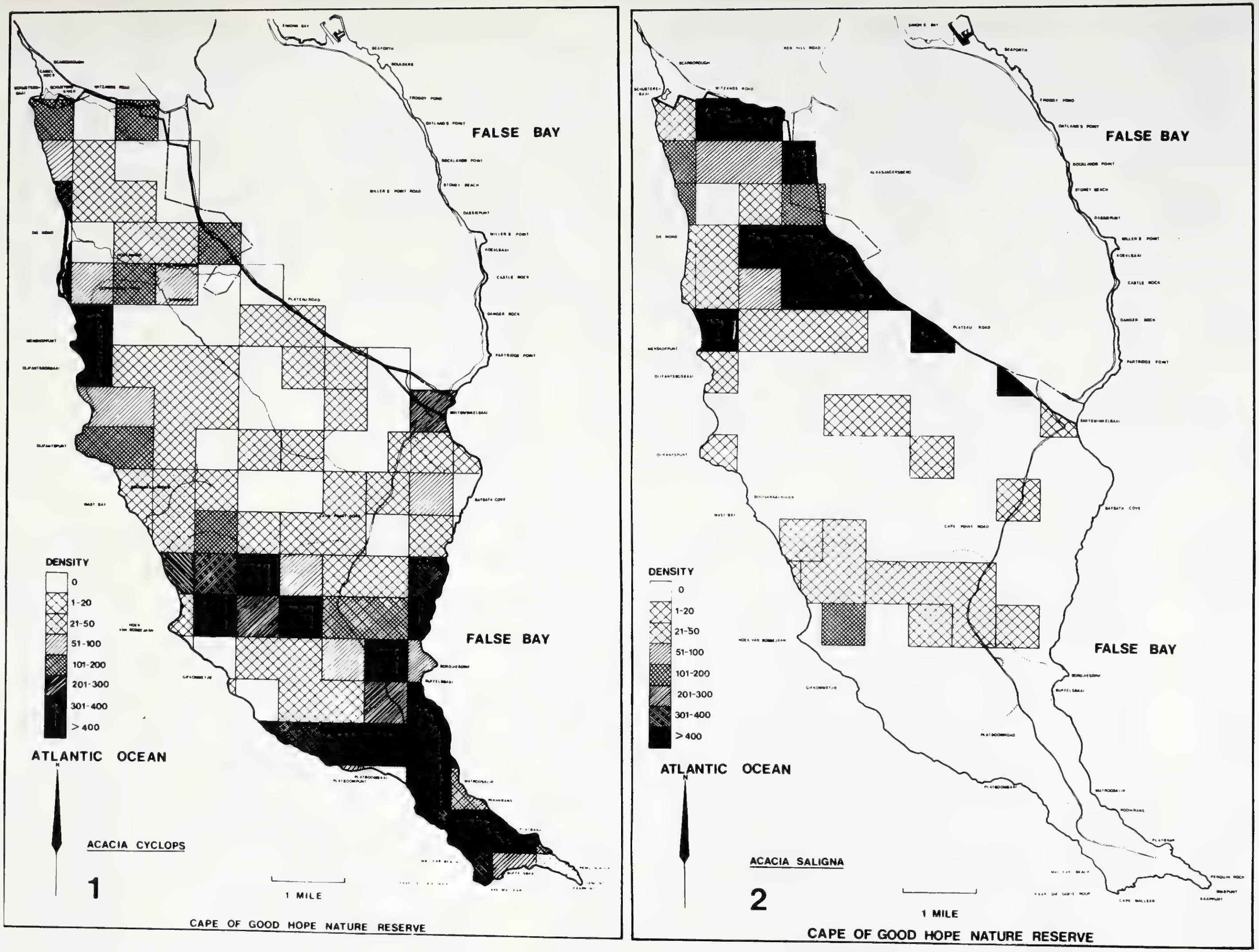

FIG. 9.—Distribution in 1966 of: 1, *Acacia cyclops;* 2, *A. saligna.*

Reserve and severely restricted to two small colonies which are in imminent danger of extinction. *Staavia dodii* (Fig. 2), also endemic to the Reserve but not as seriously threatened, occurs on the rocky hills bordering the plateau. *Mimetes hirtus* (Fig. 8) is rather rare in seepages in the northern part of the Reserve but is more common beyond its borders, on the coastal shelf across False Bay.

INVASIVE PLANTS

In the early decades of this century when smallhold farming in the southern Peninsula became uneconomic, alien woody species that had been planted as windbreaks, shade trees and sand stabilizers developed into inpenetrable thickets on the abandoned lands and then, aided by fire, spread unchecked into the adjoining veld. Because of the competitive advantage that these invasive plants have over the native flora, especially by their rapid regeneration and efficient establishment after fire, each successive burn increases their range and density to the detriment of the natural vegetation. Chief offenders on the Reserve are the Australian wattles *Acacia cyclops* (Fig. 9.1), *A. saligna* (Fig. 9.2) and *A. longifolia,* followed by *Pinus pinaster, Leptospermum laevigatum, Eucalyptus* species and *Hakea suaveolens.* During my survey in 1966–67, only 10% of the sampling sites on the Reserve, each with a 183 m radius, were completely free of alien plants.

A programme to combat their spread has since been initiated and good progress is being made, but the eradication of these invasive species remains a serious and costly management problem.

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The plant ecology of the farm Groothoek, Thabazimbi District. I. Ordination

R. H. WESTFALL*, N. VAN ROOYEN** and G. K. THERON**

ABSTRACT

The vegetation of the farm Groothoek, Thabazimbi District, situated in the Sour Bushveld (Acocks, 1975) of the Waterberg, Transvaal, is classified according to the Braun-Blanquet method and the communities are ordinated by means of detrended correspondence analysis (DCA). Five major vegetation types with 22 communities are described in terms of habitat factors, relevant to the ordination.

RÉSUMÉ

L'ÉCOLOGIE VÉGÉTALE DE LA FERME GROOTHOEK DANS LE DISTRICT DE THABAZIMBI.
1. PROGRAMMATION

Le végétation de la ferme Groothoek dans le District de Thabazimbi, situé dans le Sour Bushveld (Acocks, 1975) de Waterberg au Transvaal, est classée suivant la méthode Braun-Blanquet et les formations végétales sont programmées au moyen de l'analyse DCA (detrended correspondence analysis). Cinq types majeurs de végétation avec 22 formations végétales sont décrits selòn leur habitat, en fonction de la programmation.

INTRODUCTION

The plant ecology of the farm Groothoek in the Thabazimbi District was studied in order to supply data on the Sour Bushveld (Acocks, 1975), for the Department of Agriculture and Fisheries resource inventory. This veld type is found mainly in the Waterberg of the Transvaal and little is known about the vegetation. The study included classification of the vegetation and correlation of the vegetation with the environment to facilitate later study of the entire Waterberg region.

Van der Maarel (1980) recommends the use of ordination as an aid to classification and to help explain environmental influences. The detrended correspondence analysis (DCA) method of ordination (Hill & Gauch, 1980) is used for this study as it overcomes the problem of the 'arch effect' produced by the principal component analysis (PCA) and reciprocal averaging (RA) methods of ordination (Greig-Smith, 1980; Hill & Gauch, 1980 and Van der Maarel, 1980).

STUDY AREA

The study area consists of the farm Groothoek 278 KQ situated between 24° 28′ and 24° 31′ south latitude and 27° 32′ and 27° 39′ east longitude. The farm covers approximately 4 000 ha over an altitudinal range of 1 200 m to 2 100 m. The summit of Kransberg forms the northern boundary with the greatest farm area consisting of two plateaux at approximately 1 500 m and 1 200 m altitude to the south. Bakker's Pass lies to the west allowing vehicular access to the upper plateau.

The Kransberg Massif consists of sandstone from the Kransberg Series of the Waterberg System. Outcrops of sandstone, shale and conglomerate from the Nylstroom Series of the Waterberg System, are found on the upper plateau while sandstone outcrops are found on the lower plateau. A diabase dyke, of post-Waterberg age, is exposed in Bakker's Pass. The soils arising from these parent materials are mainly of the Mispah Form Mispah Series.

The study area is representative of Acocks's (1975) Sour Bushveld in a relatively undisturbed condition with sufficient variation in vegetation and environment for observations to be relevant to other areas in the Waterberg where this veld type occurs.

CLIMATE

The Waterberg is classified as Cwa according to Köppen's classification (Schulze, 1947), although this is not supported by direct evidence as no full climatological station has ever been maintained in the area. Rainfall statistics indicate the area as falling under the category Cw, warm temperate with summer rainfall, and the high probability that the January mean exceeds 22°C indicates the Cwa classification (Schulze, 1947). Rainfall records for the ten-year period July 1963 to June 1973 on the upper plateau suggest a mean annual rainfall of 680 mm. The consensus of local opinion, however, is that this period was unusually dry.

METHODS

The Braun-Blanquet method of sampling and synthesis followed in the study is described by Westhoff & Van der Maarel (1973), Mueller-Dombois & Ellenberg (1974) and Werger (1974).

The vegetation was stratified according to physiognomic-physiographic units determined by interpretation of 1: 33 000 aerial photographs of the study area. Sampling sites were selected by means of random co-ordinates within each physiognomic-physiographic unit. This procedure is accommodated within the flexible Braun-Blanquet method

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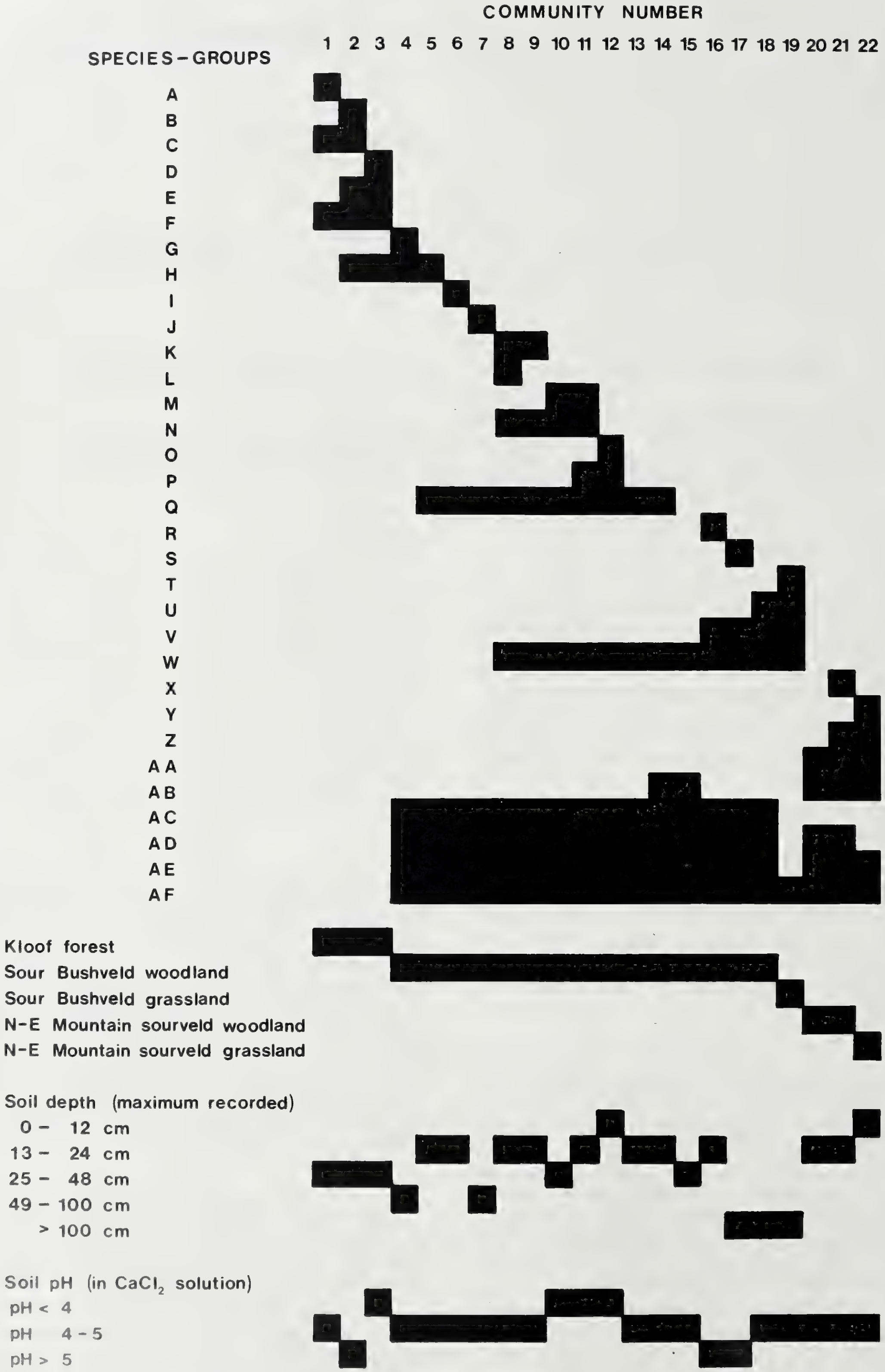

FIG. 1.—A simplified classification of the vegetation of the farm Groothoek, Thabazimbi District showing the main environmental factors according to the ordination.

(Coetzee, 1975). 170 quadrats, 10 × 20 m, were sited in homogeneous stands representing the different physiognomic-physiographic units. The 10 m × 20 m quadrat size used is considered adequate for bushveld vegetation (Coetzee *et al.*, 1976; Van der Meulen, 1979).

Data recorded at each sampling site include the species present in each quadrat with estimated canopy cover-abundance according to the Domin-Krajina scale (Mueller-Dombois & Ellenberg, 1974), altitude, geological formation, aspect, slope, soil depth, soil form and series, geomorphology, vegetation formation class and estimated percentage rock cover.

The vegetation is classified according to the Braun-Blanquet method using the PHYTOTAB program package (Westfall, Dednam, Van Rooyen & Theron, 1982). The main environmental factors influencing the communities were ordinated on floristic data by detrended correspondence analysis (DCA) (Hill & Gauch, 1980) using the DECORANA program (Hill, 1979).

RESULTS AND DISCUSSION

Classification of the vegetation, according to the Braun-Blanquet method, revealed five major vegetation types with 22 plant communities. A simplified classification of communities together with habitat factors found to be relevant in the ordination, is shown in Fig. 1.

The five major vegetation types (Fig. 1) are as follows:

(i) Kloof forest in moist, sheltered habitats (Communities 1–3).

(ii) Woodland, representative of Acocks's (1975) Sour Bushveld, on moderately deep to deep soils in moderately exposed habitats (Communities 4–18).

(iii) Grassland, representative of Acocks's (1975) Sour Bushveld on moderately deep soils in exposed, dry habitats (Community 19).

(iv) Woodland, representative of Acocks's (1975) North-Eastern Mountain Sourveld on moderately shallow soils in moderately exposed habitats (Communities 20–21).

(v) Grassland, representative of Acocks's (1975) North-Eastern Mountain Sourveld on shallow, rocky soils in exposed habitats (Community 22).

The North-Eastern Mountain Sourveld communities (Acocks, 1975) are outliers of this veld type and are found above 1 500 m altitude on the Kransberg Massif.

The results of the DCA ordination are shown in Figs 2 & 3. Communities are placed in cells, either alone, or with similar communities according to the x, y and z axes of the ordination. Fig. 2 shows the ordination of axes x and y (first and second axes) and Fig. 3 shows the ordination of axes x and z (first and third axes). The gradient of length for the x-axis is 9,25 sd, for the y-axis 4,23 sd and for the z-axis 2,69 sd where the value sd is defined so that the root-mean-square, standard deviation is 1 (Hill, 1979).

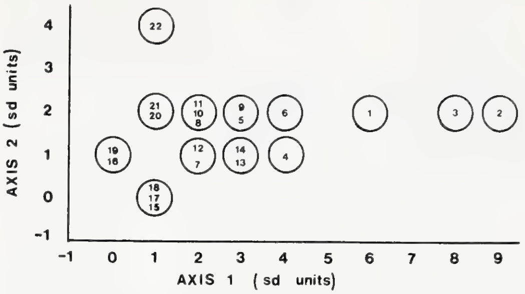

FIG. 2.—A detrended correspondence analysis (DCA) ordination of communities. Scatter diagram with communities grouped into cells along the first and second axes (z and y axes) of the ordination.

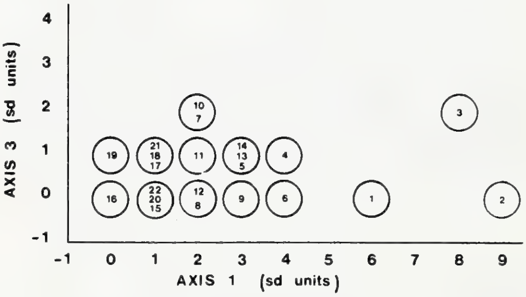

FIG. 3.—A detrended correspondence analysis (DCA) ordination of communities. Scatter diagram with communities grouped into cells along the first and third axes (x and z axes) of the ordination.

Separation of cells along axis 1 (x-axis) shows a gradient from grassland and open woodland (Communities 16 and 19) on the left to closed woodland and forest (Community 2) on the right (Fig. 4). Although no data concerning the moisture status of the communities were recorded, this gradient probably corresponds with a temperature/moisture gradient (Theron, 1973). This would range from the exposed areas of the plateau and summit grasslands and woodlands with wide temperature and moisture fluctuations, on the left of the scatter diagrams to closed woodlands and forests of the sheltered slopes and kloofs with narrow temperature and moisture fluctuations, on the right.

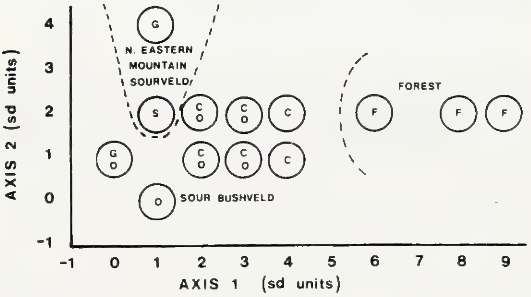

FIG. 4.—The position of five major vegetation types along the first and second axes of ordination. The first axis represents a temperature/moisture gradient from grassland to forest. G = grassland, S = sparse woodland, O = woodland, C = closed woodland and F = forest.

Community 22 (summit grassland) is more exposed than Community 19 (plateau grassland) but, because of the occurrence of mist on the summit, more moisture is received by Community 22 than Community 19. Furthermore, Community 19 is possibly subjected to inversion of temperature at night, because of slopes to the north and south, and therefore probably experiences a greater temperature range, than Community 22. The communities are consequently separated on the x-axis with Community 19 occupying the most extreme position (Fig. 2).

Separation of cells along axis 2 (y-axis) shows a general correlation with maximum recorded soil depth per cell (Fig. 5). This ranges from shallow soil (Community 22) at the top of the scatter diagram to deep soil (Communities 15, 17 and 18) at the bottom. The occurrence of Communities 16 (open woodland) and 19 (grassland) in one cell may be attributed to the underlying rock formation found with Community 19 which is impermeable shale that causes a high water-table to form during the rainy season.

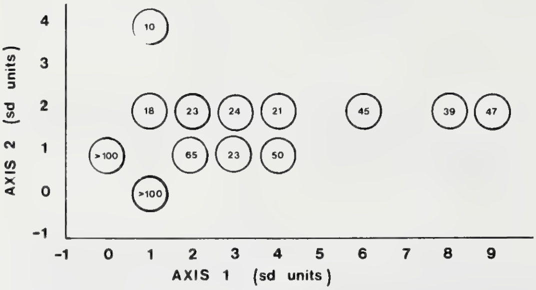

FIG. 5.—The maximum recorded soil depth, in centimetres in the community cells (Fig. 2). The second axis represents a soil depth gradient from deep soil to shallow soil.

The soil is generally deep, but where it is shallow water remains on the surface for long periods after rain. This seasonally high water-table could have the same limiting effect on root penetration as shallow soil by inhibiting growth of deep roots. The position of Community 19 on the y-axis indicates that the effective, maximum soil depth for root penetration, is under 100 cm and not over 100 cm as recorded. The position of Communities 12, 13, 14 and 16 at 1 sd unit on the y-axis and Community 15 at 0 sd units on the y-axis (Figs 2 & 5) suggests that the possible, maximum soil depth for these communities was not sampled, although the separation of cells in the centre of the scatter diagram (Figs 2 & 3) are not necessarily significant (Hill, 1979). The maximum recorded soil depths per cell on the y-axis (Fig. 5) for each sd unit, are similar to the soil depth classes which were determined on the basis of the floristic classification (Fig. 1), a comparison of which appears in Table 1.

Separation of cells along axis 3 (z-axis) shows a general correlation with mean soil pH per cell, determined in a $CaCl_2$ solution (Fig. 6). This ranges from low pH values at the top of the scatter diagram to high pH values at the bottom (Fig. 6). According to Peech (1965) soil pH, determined in a $CaCl_2$ solution, is a better indication of base saturation and is less influenced by biological and meteorological conditions, than soil pH, determined in a water solution. Soil pH determined in a water solution showed a poorer correlation with the cells along axis 3 than soil pH determined in a $CaCl_2$ solution, which supports Peech's (1965) observation.

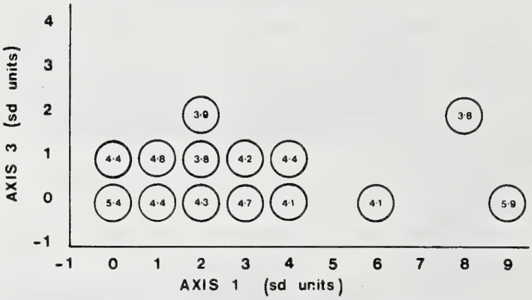

FIG. 6.—The average soil pH, determined in a $CaCl_2$ solution in the community cells (Fig. 3). The third axis represents a pH gradient from high soil pH values to low soil pH values.

Communities 3, 7, 10 and 11 have a low soil pH of under 4 (Fig. 6) indicating a high base saturation (Daubenmire, 1974). This can be partly attributed to the presence of aluminium in the soil (Daubenmire, 1977), which exceeded 1,5 me % for Communities 3, 10 and 11 and represents the highest values recorded for aluminium in the study area.

All recorded habitat data were compared with the first, second and third axes of the ordination. Apart

TABLE 1. — Soil depth classes based on ordination and floristic classification

Position of y-axis (sd units) (Fig. 5)	Maximum soil depth range (Fig. 5)	Soil depth classes based on floristic classification
4	0–10 cm	0–12 cm
2	18–47 cm	13–48 cm
1	50–65 cm (excluding Communities 13, 14 and 19)	49–100 cm
0	>100 cm	>100 cm

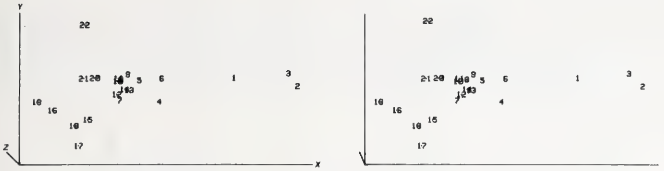

FIG. 7.—A stereogram of the three axes of ordination (x, y and z axes) according to Fewster & Orlóci (1979) for viewing with a pocket stereoscope.

from maximum recorded soil depth the inferred temperature/moisture correlation and soil pH in a $CaCl_2$ solution, either none or only partial correlation could be found. As only the first, second and third axes were considered for the main environmental gradients, other, lesser factors could show correlation with the fourth axis. However, the gradient of length for the third axis shows little separation of the cells, being only 2,69 sd (Fig. 6), whereas separation of cells on axes 2 and 1 are 4,23 sd and 9,25 sd respectively. The significance of the third axis is, therefore, considerably less than that of axes 1 and 2 while axis 4, at 2,23 sd, is of even less significance for the main environmental gradients (Hill, 1979). The first three axes of the ordination are combined in a stereogram, according to the method of Fewster & Orlóci (1978) for three-dimensional viewing (Fig. 7) with the aid of a pocket stereoscope.

The five major vegetation types revealed in the classification (Fig. 1) are also present in the ordination (Fig. 4). Forest communities are separated to the right of the scatter diagram, with Sour Bushveld grassland to the left. The Sour Bushveld woodland vegetation is represented by the cells in the centre of the scatter diagram ranging from open woodland to the left, to closed woodland to the right. The North-Eastern Mountain Sourveld grassland on shallow rocky soil is separated on axis 2, above, with North-Eastern Mountain Sourveld woodland directly below. The Sour Bushveld open woodland vegetation on deep soil is represented by the cells at the bottom of axis 2.

CONCLUSIONS

The ordination of communities confirms the five major vegetation types found in the vegetation classification according to the Braun-Blanquet method. The main environmental gradients influencing these vegetation types are soil pH, soil depth and apparently a temperature/moisture gradient. The possibility of estimating moisture available to vegetation, although difficult to establish in surveys where sampling sites are only visited once, should nevertheless, receive more attention. Finally, the ordination shows discontinuities in the vegetation, hence the need for a classification.

ACKNOWLEDGMENTS

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Aspects of an experimental study on root aerenchyma development and the ecological implications thereof

J. HARDCASTLE* and K. H. SCHUTTE*

ABSTRACT

Anaerobic conditions induced cortical aerenchyma in maize roots cultivated in water culture. Similar results were obtained by growing the plants in nitrate and phosphate deficient solutions but the cavitation was more severe when conditions were anaerobic. Low temperatures delayed the onset of these symptoms. Mineral deficiencies also regulated the formation of root hairs in water culture. In the field, the behaviour of the rooting systems in a group of Restionaceae with aerenchyma was interpreted from anatomical and developmental data.

RÉSUMÉ

ASPECTS D'UNE ÉTUDE EXPÉRIMENTALE SUR LE DÉVELOPPEMENT DE L'AÉRENCHYME RADICULAIRE ET DES IMPLICATIONS ECOLOGIQUE QUI EN DÉCOULENT

Les conditions anaérobiques ont induit l'aérenchyme cortical de racines de maïs cultivées en aquiculture. Des résultats similaires ont été obtenus en cultivant des plantes dans des solutions déficientes en nitrate et en phosphate mais la formation de cavités était plus importante quand les conditions étaient anaérobiques. De basses températures retardèrent le déclenchement de ces symptômes. Les déficiences minérales réglèrent aussi la formation des poils radiculaires en aquiculture. En champ, le comportement des systèmes radiculaires dans un groupe de Restionaceae avec aérenchyme fut interprété à partir de données de développement et de données anatomiques.

INTRODUCTION

Root aerenchyma is a characteristic feature of many submerged water and marsh plants. These root cavities are classically regarded as reservoirs which facilitate the active diffusion of oxygen into the interior of the root (Williams & Barber, 1961).

One of the fundamental characters of anaerobiosis is the change in the root environment resulting from the marked change in the redox potential of the soil solution. This means that not only is there a decrease in the availability of oxygen in the soil but the availability of nutrients to the plant becomes drastically altered. Such variations in the root environment are reflected in differential growth responses of the root. Growth responses of roots are particularly striking as their lack of determinate structures enables a researcher to observe degrees of phenotypic plasticity in root morphology. This has led to the traditional concept of anaerobic responses of the roots in the field and in the laboratory as the formation of aerenchyma and a thickened, shortened root (Bryant, 1934; McPherson, 1939) with a marked decrease in root hair development (Williams & Barber, 1961).

Recently, interest has been revived in the ontogeny of aerenchyma (Kawase, 1979; Konings & Verschuren, 1980). Our studies of the ontogeny of root aerenchyma show degrees of cavitation; the patterns of cavitation are predictable but more variable than we initially expected. Since this variation appeared to be coupled to environmental conditions, we decided to study it further.

Our initial aim was to investigate the parameters regulating aerenchyma development. It was soon clear to us, however, that oxygen tension was not the only factor inducing the formation of aerenchyma. As anaerobiosis limits the uptake of nutrients in plants we decided to determine the role of nutrient deficiencies in inducing aerenchyma formation. Initially our research material was *Zea mays,* in which cavitation was readily induced by growing it in water culture solutions lacking essential nutrients such as nitrogen or phosphorus. Efforts were made to prevent aerenchyma formation in plants which normally exhibit it, using the same water culture techniques. Here the plasticity of cavitation was investigated using *Elegia capensis,* one of the Restionaceae.

The ecological significance of aerenchyma formation in a few selected key species of the Fynbos Restionaceae from Pella (the Fynbos Biome Research site 80 km north of Cape Town) was investigated in the field and in the laboratory. As the Restionaceae are a large group of plants about which there is scant physiological data and which are very difficult to manipulate experimentally, our results are preliminary and tentative.

METHODS

Water culture techniques were employed for the cultivation of *Zea mays* and *Elegia capensis* using the Long Ashton solution (Hewitt & Smith, 1975). *Zea mays* plants were cultured 7 days after germination and the roots sampled 10 days later. Plants of *Elegia capensis* were approximately 4 months old when cultured and the material was sampled after 3 months.

RESULTS

Induction of cavitation in Zea mays

Variations in cavitation patterns developed under different regimes are shown in Fig. 1. In this study it

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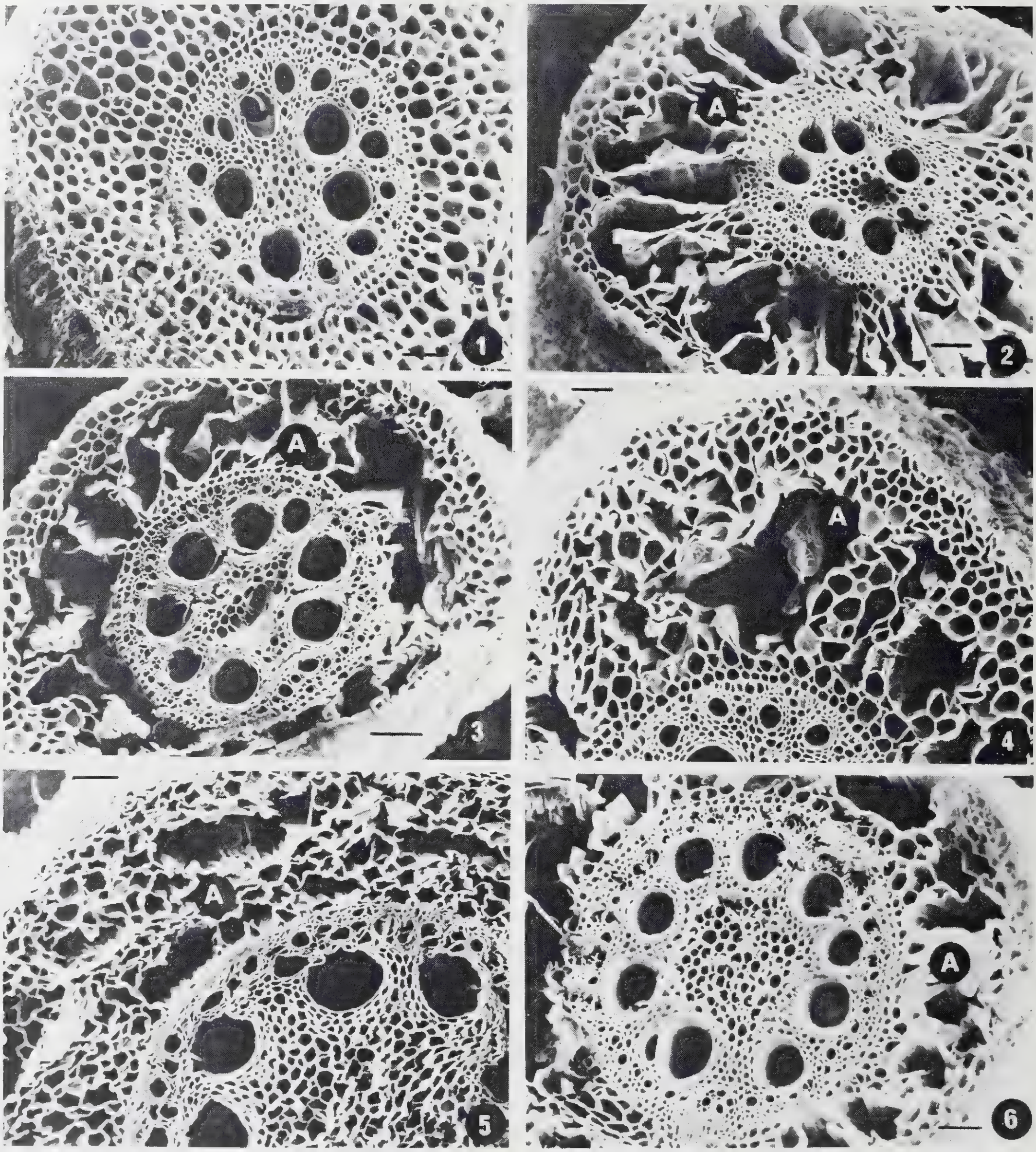

FIG. 1.—Comparison of root cortical development in *Zea mays* under varying experimental regimes. Bar = 100 μm. 1, Control, full nutrient solution, aerobic conditions; 2, Control, distilled water only, aerobic conditions; 3, Nitrate deficient medium, anaerobic conditions; 4, Nitrate deficient medium, aerobic conditions; 5, Phosphate deficient medium, anaerobic conditions; 6, Phosphate deficient medium, aerobic conditions. A = Aerenchyma.

was noted that the occurrence of aerenchyma, in relation to the root tip, varied markedly depending on the nutrient deficiency and ambient temperatures. These results are shown in Table 1.

Our experimental results show that the rate at which aerenchyma appears is related to the availability of nutrients and that this availability is modified by aeration of the substrate. Low temperatures slow down the plant metabolism of the plant and the distance, from the root apex at which cavitation is first noted, is far greater than that determined at higher temperatures. Aerenchyma develops earlier in roots under anaerobic treatments regardless of the nutrient deficiency in the culture medium.

Induction of non cavitation in Elegia capensis

Elegia occurs in swamps with exceptionally low nutrient levels. We were unable to cultivate it in standard nutrient media (water culture methods). It does, however, thrive in water culture with only micronutrients added. Aerenchyma formation is repressed in aerated solutions.

These simple experiments show that the rooting systems can be manipulated to induce or repress cavitation and that certain factors such as oxygen

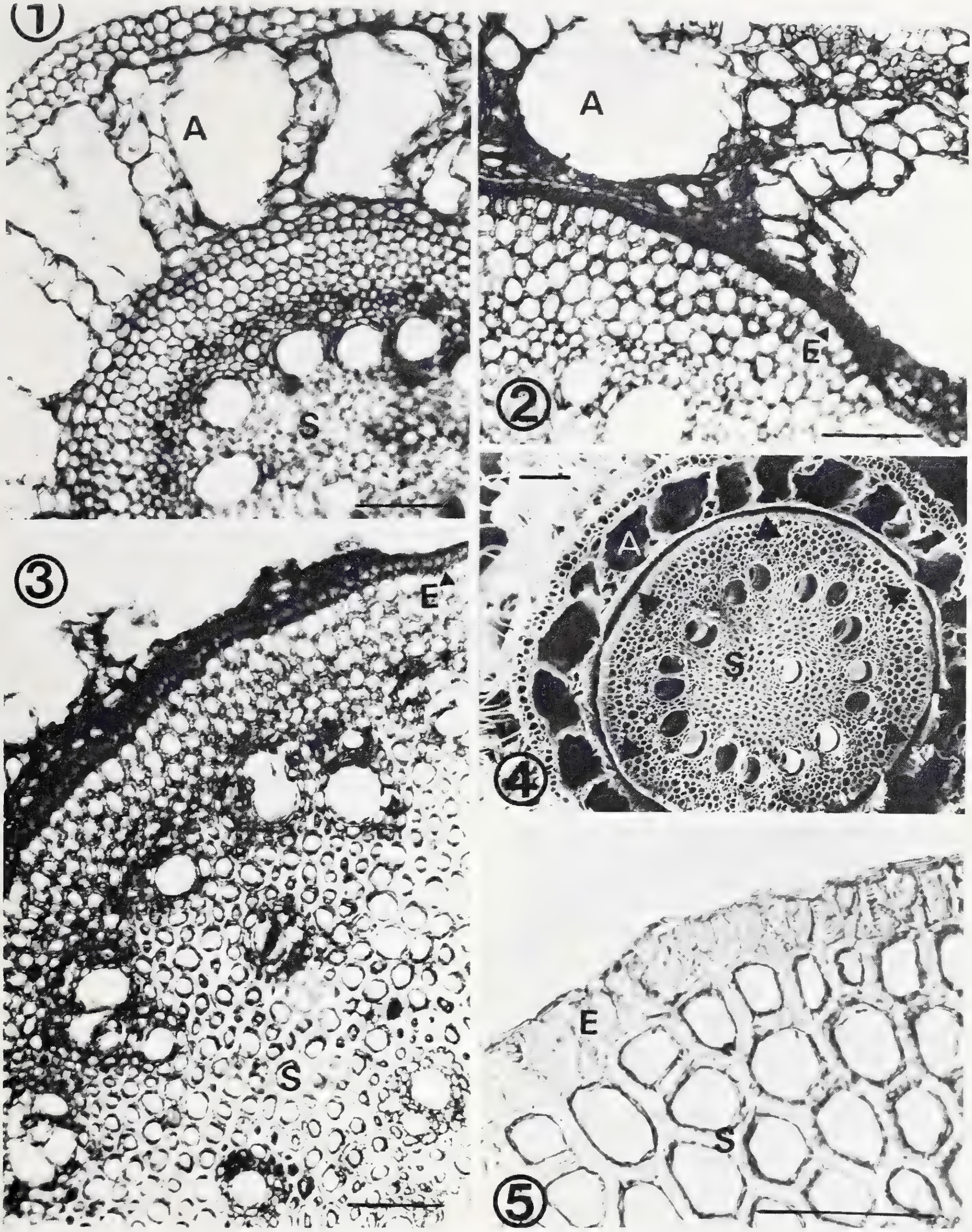

FIG. 2.—Root development in *Cannamois* showing possible relationship between thick and thin roots. Bar = 100 μm. 1, Transverse section of thick root showing initial aerenchyma development; 2, Transverse section of thick root showing thickened cells of the endodermis and cortical region; 3, SEM micrograph showing initial stage (see arrows) in the 'sloughing off' of the cortical region. Note dense roothairs; 4, Transverse section of thin root showing remnants of the cortex adjacent to the endodermis; 5, Transverse section of thin root showing thickened endodermal cells. A = aerenchyma; E = endodermis; S = stele.

TABLE 1.—A comparison of the effects of nutrient deficiencies on aerenchyma formation in *Zea mays* grown in aerobic or anaerobic water culture for 10 days at two different temperature regimes. The formation of aerenchyma was related to the distance in mm, from the root apex at which cavitation was first noted

		Temperature 28° C		Temperature 12° C	
		Aerated solution	Non-aerated solution	Aerated solution	Non-aerated solution
Nutrient deficiency	Nitrate	25	15	60	44
	phosphate	28	20	152	130
Control	Distilled water	20	10	40	27

Sample size 20 plants per treatment. SD = 1,23

tension, nutrient status and temperature are clearly implicated. Armstrong (1971) came to similar conclusions and his studies on rice showed that 'the extensive gas-space development in the roots is an obvious response to conditions associated with soil anoxia and may be delayed, reduced or even prevented if the soil is made aerobic.'

ECOLOGICAL IMPLICATIONS

The specific adaptations of plants to cope with conditions of nutrient imbalance is still speculative (Epstein, 1972). Aerenchyma formation is an obvious adaptation to the wetland condition and it is at best only poorly developed in non-wetland species (Armstrong, 1979). The occurrence of aerenchyma in the Restionaceae is well documented (Cutler, 1969) and rooting strategies are currently under investigation (Stock, 1981). The root systems of *Elegia, Wildenowia, Cannamois* and *Hypodiscus* are among those that are being investigated in this study.

The group comprising *Wildenowia, Cannamois* and *Hypodiscus* exhibit two types of roots during the spring and winter months, thick fleshy roots commonly referred to as 'feeding roots' and thin fibrous roots. In *Cannamois* the thick roots are approximately 5 mm in diameter and the thin roots 1,5 mm in diameter. Our studies of *Cannamois* during spring and winter reveal the rapid production of new foliage, active growth of the thick roots, with concomitant aerenchyma development (Fig. 2.1) and a high transpiration rate of ,4g/dm^2/h. [cf. *Citrus* ,7g/dm^2/hr (Salim & Todd, 1965)]. It would appear that these thick aerenchymatous roots are produced in response to lower soil temperatures (Stock, 1981), low nutrient status (Stock, 1981) and an anaerobic root environment as a result of persistent winter rain. As seasonal temperatures rise, the soil dries out thereby improving aeration of the substrate, the aerenchymatous cortex is characterized by marked suberization and lignification of the cells (Fig. 2.2). Finally, the cortex disintegrates and is 'sloughed off' (Fig. 2.3) resulting in the thin fibrous type of root (Fig. 2.4). In this root the endodermis is markedly thickened (Fig. 2.5) and appears to be 'waterproofed' as a result of lignin and suberin deposits thereby sealing off the central stele during the summer months. This then forms the thin fibrous root noted when sampling material and could therefore represent the previous year's growth.

By comparison, *Elegia* occurs in permanently moist soils in swamp-like areas and has been noted to have a predominance of the thick fleshy aerenchymatous type of root throughout the year in marked contrast to that noted in the above mentioned species. As *Elegia* is not subjected to the periodic gradual drying out of the root environment, the aerenchymatous cortex remains intact. These thick roots were manipulated during initial studies.

At this stage the whole phenomenon of root aerenchyma development appears to be associated with the water relations and nutrient supply of the plant. Aerenchyma development demonstrates a rapid, plastic response to the environment with fascinating ecological and physiological implications.

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Bothalia 14, 3 & 4: 795–798 (1983)

Cytotaxonomic studies in African Asclepiadaceae

F. ALBERS*

ABSTRACT

The family Asclepiadaceae of about 290 genera is a homogeneous complex with complicated flower-structure. Little cytological data are available on the approximately 3 000 species in the family. The best studied subtribe is the Ceropegiinae (*sensu* Schumann, 1895) including the Stapelieae (as presently recognized) with its dominantly succulent members. Exactly half of the species are known karyologically. The basic chromosome number in the family is x = 11 and in most of the genera polyploid taxa are also to be found. The small size of the chromosomes makes individual identification very difficult and they form a graded series with very slight morphological differences. C-banding permits identification of heterochromatic regions; they all take up near centromeric positions. Therefore, studies aimed at an analysis of relationships with the aid of chromosome morphology on a lower taxonomic level, will hardly be possible. In so far as morphological characters of the inflorescence are concerned, diploid species of the genus *Caralluma* seem to form a species centre in South Arabia/East Africa.

RÉSUMÉ

ÉTUDES CYTOTAXONOMIQUES CHEZ LES ASCLÉPIADACÉES AFRICAINES

La famille des Asclépiadacées, comptant environ 290 genres, est un complexe homogène avec une structure florale compliquée. Peu de données cytologiques sont disponibles sur les quelque 3 000 espèces de la famille. La sous-tribu la mieux étudiée est celle des Céropégiinées (sensu *Schumann, 1895) incluant les Stapéliées avec la plupart de ses membres succulents. Exactement la moitié des espèces sont connues caryologiquement. Le nombre de chromosomes de base dans la famille est x = 11 et dans la plupart des genres, des taxons polyploïdes peuvent aussi se recontrer. La petite taille des chromosomes rend l'identification individuelle très difficile et ils forment une série progressive avec de très faibles différences morphologiques. Le C-banding permet l'identification des régions hétérochromatiques; elles se situent toutes, à proximité du centromère. Par conséquent, les études qui ont pour but d'analyser les affinités à l'aide de la morphologie du chromosome à un niveau taxonomique inférieure, seront difficilement possibles. Pour autant que les caractères morphologiques de l'inflorescence soient concernés, les espèces diploïdes de genre* Caralluma *semblent former un centre de speciation dans le Sud de l'Arabie et l'Afrique de l'Est.*

The basic scheme for the infrafamilial classification of Asclepiadaceae was laid down by Robert Brown as early as 1811. Most workers have subsequently accepted this classification with few deviations, but names and taxonomic ranks have changed considerably.

Schumann's (1895) systematic classification, based directly on Brown's original key to the genera of Asclepiadaceae, is used in the classification adopted in Table 1. The few chromosome numbers published in the various subtribes indicate that little cytological data are available for taxa distributed throughout the world, except for some more detailed studies of the succulent members of the subtribe Ceropegiinae. Of the 290 genera with about 3 000 species, only 342 species in 52 genera are known karyologically, i.e. only 11% of the species. The basic chromosome number in the family is x = 11 and the literature reveals few numbers deviating from this, such as 10 and 12.

Cytotaxonomically, the best-studied subtribe is Ceropegiinae, which is, with few exceptions, well characterized by pollinia with a special germination area and winged caudicles (Schill & Jäckel, 1978). It is represented in southern Africa by members of the genera *Orthanthera* Wight, *Brachystelma* R. Br., *Dichaelia* Harvey, *Ceropegia* L., *Riocreuxia* Decne, and by an allied group formed by the stapeliads. In the last-mentioned group, with exclusively succulent-stemmed members, karyological work was started by Reese in 1967. The data given in Table 2 are from the later publications of Reese (1971) and the present author (1974, 1975, 1976, 1977, 1981). The present taxonomic situation proposed by Leach (1975, 1978, 1980) merits comment. Previous classification in stapeliads has been based mainly on floral characters, particularly those of the corona, the inner part of the flower. The division on coronal characters has resulted in a most unsatisfactory situation, particularly at sectional and generic level. We are now aware that the corona is a very variable structure, and its usefulness as a major character in taxonomic work is therefore diminished. In an effort to obtain a more natural classification, particularly at generic level, Leach has paid more attention to vegetative characters such as the form of the stems and arrangement of the leaves. The result is that some genera such as *Orbeopsis, Pachycymbium* and *Orbeanthus* have had to be set up, or reinstated such as *Orbea* and Haworth's long-forgotten genus *Tridentea.* Other genera, for example *Echidnopsis, Hoodia, Huernia* and *Piaranthus* are readily distinguishable by vegetative and floral characters.

Each of the 11 genera mentioned in Table 2 contains more than 10 species; the largest with 120 species is the genus *Caralluma.* In the remaining 11 genera there are 47 species. The chromosome numbers of exactly half the species are known. In many of the taxa only one plant could be studied. Investigations in some species have shown that

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TABLE 1.—Taxa of the Asclepiadaceae with known chromosome numbers

Taxa	No. of species with known chromosome number	No. of genera involved
Periplocoideae		
tribe Periploceae	7	4
Cynanchoideae		
tribe Asclepiadeae		
subtribe Astephaniae	—	—
Glossonematinae	2	2
Asclepiadinae	33	5
Cynanchinae	19	5
Oxypetalinae	—	—
tribe Secamoneae	1	1
tribe Tylophoreae		
subtribe Ceropegiinae	**261**	**25**
Marsdeniinae	18	9
tribe Gonolobeae	1	1
Total	342	52

TABLE 2.—Genera of the stapeliads with known chromosome numbers in various ploidy levels

Stapeliad genera	Known number of species	% of karyol. known species	Number of species with 2x 22	4x 44	6x 66	10–12x 110–132
Caralluma	120	50	52	3	2	3
Duvalia	20	55	4	6	1	—
Echidnopsis	25	60	13	2	—	—
Hoodia	15	33	5	—	—	—
Huernia	60	71	36	6	1	—
Orbea	20	45	4	5	—	—
Orbeopsis	10	60	5	1	—	—
Piaranthus	15	53	7	1	—	—
Stapelia	75	44	30	2	1	—
Tridentea	17	47	8	—	—	—
Trichocaulon	15	26	4	—	—	—
+ 11 genera	47	42	18	2	—	—
Total	439	50	186	28	5	3

polysomaty of different kinds can be observed quite often (Reese, 1973) and, in addition, polyploid adventitious roots arising from shoots lying on the ground are rather frequent (Albers, 1979). The occurrence of these cytological and morphological features complicates the determination of the chromosome numbers. Further, in half of the genera polyploid taxa are to be found with chromosome numbers from 44–132, but only in genus *Duvalia* do polyploids play an important part, whereas in other genera the percentage of polyploidy is rather low.

A comparison of polyploidy levels in stapeliads with that of the non-succulent members of the family shows that the stapeliads have a higher proportion of species with high polyploid levels (Table 3).

In Fig. 4 metaphase plates in root tips with different chromosome numbers are to be seen showing no differences in chromosome size between the polyploid levels. The small size of the chromosomes from 1–2 μm makes individual chromosomal identification very difficult. Only Nakamura (1972) and Jash & Sharma (1972) have attempted studies in the past. Two pairs of chromosomes are clearly distinguishable, one pair as SAT-chromosomes with a NO (nucleolous organization) Region and one pair with a satellite at the distal end of the longer arm. Both pairs seem to occur in many genera as well as in non-succulent ones. The other nine pairs of chromosomes of a diploid species form a graded series with very slight morphological

TABLE 3.—A comparison of the ploidy levels of different groups in Asclepiadaceae

Asclepiadaceae group	2x	Numbers of species with 4x	6x	>6x	Percent polyploids
Stapeliads	186	28	5	3	16
Non-succulent members	110	11	—	—	9

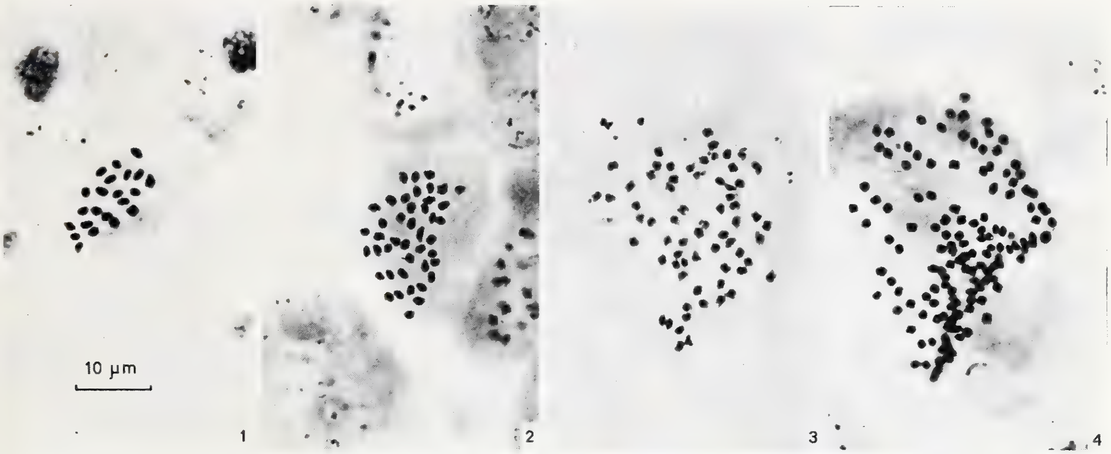

FIG. 1.—Metaphase plates in root tip cells of different species of stapeliads: 1, *Hoodia gordonii,* 2n = 22; 2, *Echidnopsis watsonii,* 2n = 44; 3, *Duvalia corderoyi,* 2n = 66; 4, *Caralluma burchardii* var. *sventenii,* 2n = 132.

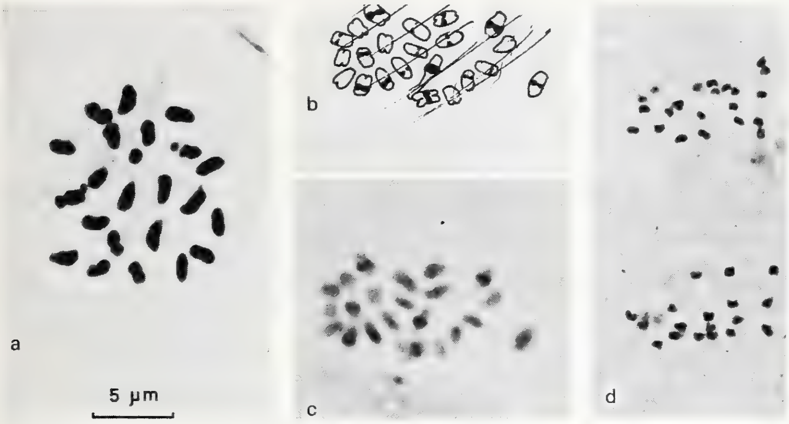

FIG. 2.—a, somatic metaphase plate of *Brachystelma dinteri* (2n = 22) with distinct chromosome morphological differentiation; b & c, C-banded metaphase plate of *Caralluma hottentotorum* (2n = 22) — b is the camera ludica drawing of the microphotograph c: d, meiotic anaphase I of *Ceropegia woodii.*

differences and median to subterminal primary constrictions (Fig. 2a).

C-banding greatly facilitates the recognition of individual chromosomes. The metaphase plate of a *Caralluma* species shows heterochromatic regions on some chromosomes (Fig. 2b & c). All heterochromatic regions are in centromeric positions. The same heterochromatic distribution is found in the SAT-chromosomes. In three pairs no heterochromatin is recognizable after Giemsa staining.

The situation in *Caralluma* is found in many of the species of Asclepiadaceae studied by the author. Further morphological diversity as shown by Jash & Sharma (*l.c.*) and Nakamura (*l.c.*) could scarcely be observed. Karyotype analysis has revealed great similarity in chromosome morphology in all the species of Asclepiadaceae studied. Therefore studies aimed at analysing relationships with the aid of chromosome morphology at a lower taxonomic level (and we have started our studies with the intention of doing so) will hardly be possible.

Though behaviour of the chromosomes in microsporogenesis allows one to draw conclusions about relationship in assumed polyploid hybrids, studies of meiotic divisions in Asclepiadaceae are very rare (Jash & Sharma, 1972; Reese, 1971) — due to various difficulties. The anaphase I of the tetraploid *Ceropegia woodii* shows a normal chromosome position (Fig. 2d). Morphological studies of inflorescences have shown that the *Caralluma-umbellata-europaea*-group in the genus *Caralluma,* which occurs north of the equator, seems to be the most primitive group (Wertel, 1976). The inflorescence-forms can be derived from a basic type, which is represented in the terminal umbels or umbels near the tip of the stem of some *Caralluma* species as can be seen, for instance, in *C. speciosa* from Somalia.

In Fig. 3 the presently known species of this *Caralluma*-group are shown in their regions. A species centre with 29 species, all diploid, is remarkable in the area of South Arabia and East Africa. Hexaploid species appear at the north-west border of the distribution range in Morocco and South Spain, where the stapeliads reach Europe. The highest known chromosome counts are from the two varieties of the endemic *Caralluma burchardii* on the Canary Islands in which 110, 121 and 132 chromosomes are to be found (Albers, 1977, 1981; Borgen, 1974, 1977; Reese 1971.)

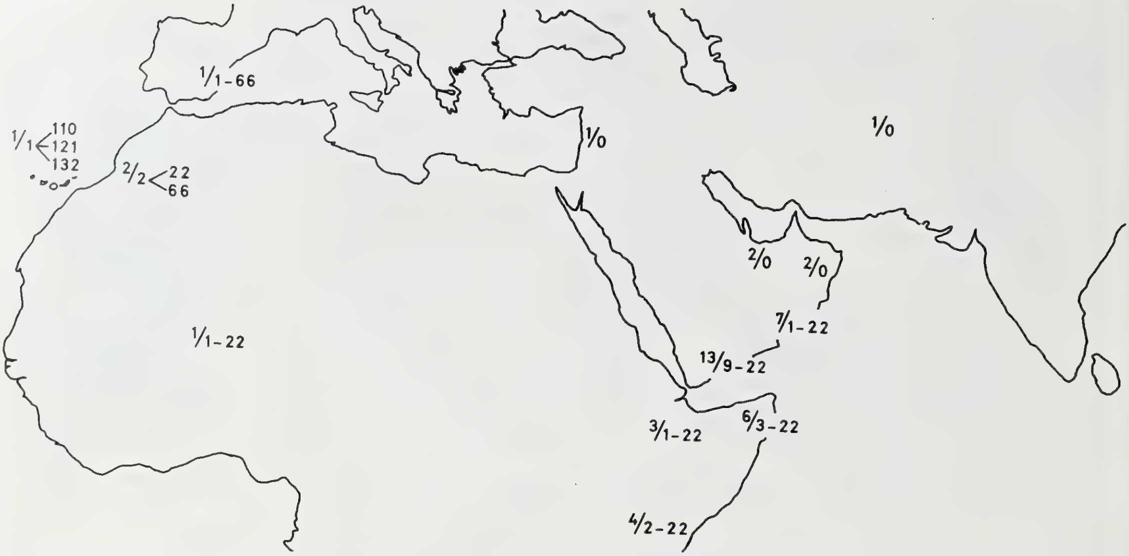

FIG. 3.—The presently known numbers of species of the genus *Caralluma* north of the equator are to be seen above the diagonal line, the karyologically known under the line, followed by the chromosome number.

If we turn to the east, we come to the species of the Indian Peninsula, which is thought to be the centre of origin of the stapeliads. This supposition may be considered to be supported by the occurrence of *Caralluma frerei* on this subcontinent, because this species is the only one with leaf-like foliage. Therefore, this species could possibly be regarded as the most primitive species. But karyology cannot support this view for, *Caralluma frerei* with 2n = 44, has a derived chromosome number, which rather conflicts with previous ideas. Unfortunately, counts of the other Indian species are as yet unknown.

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Some remarks on the taxonomy of the Plumerioideae (Apocynaceae)

A. J. M. LEEUWENBERG*

ABSTRACT

The family of the Apocynaceae is usually subdivided into two subfamilies, the Plumerioideae with the type genus *Plumeria* from tropical America, and the Apocynoideae, often named Echitoideae, with the type genus *Apocynum* from North America. These subfamilies show two characters which are more or less diagnostic for all members.

However, since the taxonomists have built up the present scheme of the Apocynaceae, phytochemists have observed that many plants belonging to the Plumerioideae contain alkaloids, and that many representatives of the Apocynoideae contain glycosides. Some of the alkaloids, e.g. those of *Catharanthus, Rauvolfia* and *Voacanga,* and some of the glycosides, e.g. those of *Funtumia* and *Strophanthus* are of medicinal interest.

In the present paper, the arrangement of the genera within the Plumerioideae is mainly that of Pichon (1949, 1950, 1953a, 1953b). He subdivided all tribes, except the Tabernaemontaneae, into subtribes, which is an excellent concept according to the present author. The latter, however, does not always agree with the delimitation of the genera. For instance, he does not accept the sinking of *Acokanthera* under *Carissa,* especially as the plants belonging to these genera show great differences in architecture (Hallé & Oldeman 1970; Hallé, Oldeman & Tomlinson, 1978), but he sinks several genera maintained by Pichon, e.g. *Ervatamia* under *Tabernaemontana* (1976).

RÉSUMÉ

QUELQUES REMARQUES SUR LA TAXONOMIE DES PLUMÉRIOÏDÉES (APOCYNACEAE)

La famille des Apocynacées est habituellement subdiviseé en deux sous-familles, les Plumérioïdées avec le genre-type Plumeria *d'Amérique tropicale et les Apocynoïdées souvent désigniées Echitoïdées, avec le genre-type Apocynum d'Amérique du Nord. Ces sous-familles montrent deux caractères qui sont plus ou moins diagnostiques pour tous leurs membres.*

Cependant, depuis que les taxonomistes ont établi la présente classification des Apocynacées, les phytochimistes ont observé que beaucoup de plantes appartenant aux Plumérioïdées contiennent des alcaloïdes, comme ceux des Catharanthus, Rauvolfia *et* Voacanga, *et certains des glycosides, comme ceux des* Funtumia *et* Strophanthus, *qui ont un intéret médicinal.*

*Dans la présente note, la classification des genres dans les Plumérioïdées est basèe principalement sur celle de Pichon (1949, 1950, 1953a, 1953b). Celui-ci subdivisa toutes les tribus, excepté les Tabernaémontanées, en sous-tribus, ce qui est un excellent concept suivant le présent auteur. Ce dernier n'est cependant pas toujours d'accord avec la délimitation des genres. Par exemple, il n'accepte pas la synonymie d'*Acokanthera *avec* Carissa, *spécialement parce que les plantes appartenant à ces genres montrent de grandes différences dans leur architecture (Hallé & Oldeman 1970; Hallé, Oldeman & Tomlinson, 1978), mais il met en synonymie plusieurs genres maintenus par Pichon, par exemple* Ervatamia *avec* Tabernaemontana (1976).

The family of Apocynaceae is usually subdivided into two subfamilies, the Plumerioideae with the type genus *Plumeria* from tropical America, and the Apocynoideae, often named Echitoideae, with the type genus *Apocynum* from North America. These subfamilies show two characters which are more or less diagnostic for all members. The corolla lobes overlap to the left in the former and to the right in the latter; the stigma and/or style are free from the anthers in the first but stick to the connectives in the second. In the latter case the falling corolla carries the stigma and style with it. Although these characters are mostly useful to distinguish between the members of these sub-families, exceptions occur, e.g. in the Plumerioideae the corolla lobes of *Carruthersia, Holarrhena, Schizozygia* and a single *Callichilia* species, *C. subsessilis,* overlap to the right. The stigma of *Voacanga* sticks to the connectives of the anthers.

However, since the taxonomists have built up the present scheme of the Apocynaceae, phytochemists have observed that many plants belonging to the Plumerioideae contain alkaloids, and that many representatives of the Apocynoideae contain glycosides. Some of the alkaloids, e.g. those of *Catharanthus, Rauvolfia* and *Voacanga,* and some of the glycosides, e.g. those of *Funtumia* and *Strophanthus* are of medicinal interest.

In the present paper the arrangement of the genera within the Plumerioideae is mainly that of Pichon (1949, 1950, 1953a, 1953b). He subdivided all tribes, except the Tabernaemontaneae, into subtribes, which is an excellent concept according to the present author. The latter, however, does not always agree with the delimitation of the genera. For instance, he does not accept the sinking of *Acokanthera* under *Carissa,* especially as the plants belonging to these genera show great differences in vegetative architecture (Hallé & Oldeman 1970; Hallé, Oldeman & Tomlinson, 1978), and he sinks several genera maintained by Pichon, e.g. *Ervatamia* under *Tabernaemontana* (1976).

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As far as is known, the representatives of the Tabernaemontaneae resemble one another much more closely phytochemically than the representatives of any of the other tribes of the Plumerioideae, e.g. the Carisseae and the Plumerieae. This observation is strongly supported by their morphology and basic structure. The Carisseae all have fleshy syncarpous fruits, but several other characters indicate that they are to be placed in several subtribes, as listed in the Appendix on p. 801 *Carissa* and *Acokanthera,* which constitute the Carissinae, have strikingly similar flowers and drupaceous fruits, but whereas *Carissa* is a repeatedly dichotomously branched shrub or climber with two large mostly branched, spines at each ramification, *Acokanthera* is an unarmed tree with a much less strict branching system. It must be stated, however, that the flowers and fruits of the two genera are so similar, that Pichon, who had no opportunity to see the living plants in the field, combined them.

The next subtribe, the Landolphiinae, which Pichon monographed (1953a), is much more uniform. The resemblance of the genera is so strong, that much confusion existed about their delimitation and interrelationship, before Pichon's excellent work was published. Although it is still difficult to distinguish the genera which he maintains, the present author is inclined to agree with him after having seen many species in the field. They all have berries, which are often tasty, e.g. these of *Ancylobotrys capensis* and *Landolphia dulcis.* In this whole subtribe, only a single architectural model occurs. Each module of a plant ends with a curled tendril, which may bear flowers. A lateral branch is a second module. The lateral branch opposite the second module may end with an inflorescence or with a never opening terminal bud. Its model strikingly resembles that of Koriba (Hallé & Oldeman, 1979; Hallé, Oldeman & Tomlinson, 1978).

The Pleiocarpinae which, like the Landolphiinae, are almost exclusively African, are remarkably similar in their flowers and fleshy indehiscent fruits. At least *Hunteria eburnea, H. ghanensis* and *Pleiocarpa mutica* have Troll's model (Hallé & Oldeman, 1970; Hallé, Oldeman & Tomlinson, 1978).

The Plumerieae show great variation, even within the subtribes. Their fruits are apocarpous and usually dry; fleshy fruits, which are even edible, are only known for *Geissospermum.* The seeds bear a terminal coma, e.g. in *Holarrhena* and *Carruthersia,* a basal and a terminal coma, e.g. in *Alstonia,* or none, e.g. in *Amsonia, Catharanthus* and *Plumeria.* Winged seeds occur in *Aspidosperma, Diplorhynchus* and *Pycnobotrya,* all three belonging, like *Geissospermum,* to the subtribe Aspidospermatinae. The known architectural models of this tribe, in which the flowers show remarkable resemblances, are that of Massart in *Aspidosperma* and that of Nozeran in *Geissospermum.*

In *Plumeria* at least two models are found, that of Koriba in *P. articulata* and that of Leeuwenberg in *P. rubra* (Hallé & Oldeman, 1970; Hallé, Oldeman & Tomlinson, 1978). In *Alstonia* at least three models can be distinguished, that of Koriba in *A. macrophylla* (also once observed by the present author in *A. boonei* in Gabon), that of Prévost in *A. boonei, A. congensis* and *A. scholaris,* and that of Leeuwenberg in *A. sericea.* Although it is difficult to decide on diagnostic characters for the Plumerieae, its subtribes appear to be quite natural.

The tribe Tabernaemontaneae, which is chemically remarkably uniform and pharmaceutically promising, is very uniform both in vegetative architecture and in fruits and seeds. All species show the model of Leeuwenberg, but mostly partly reduced. The present author only once observed the model complete in a specimen of *Tabernaemontana divaricata* in a private garden in Saul in French Guiana. The terminal inflorescence is composed of a pedicellate central flower supported by two peduncles each bearing a cyme supported by two branchlets. In all other specimens of this tribe, he observed that in the field several reductions occurred. Firstly, the terminal flower is missing, rendering the two lateral branches separate inflorescences. Secondly, one of these inflorescences, and often also one of the branchlets, may not develop. Especially in the latter case, the model cannot easily be recognized. The fruits are mostly apocarpous, fleshy and dehiscent. Syncarpous fruits occur in *Tabernanthe* and partly syncarpus fruits often occur in *Callichilia, Tabernaemontana* and *Voacanga. Schizozygia* bears dry fruits, whereas the fruits of several *Tabernaemontana* species are indehiscent, e.g. those of the Asian *T. aurantiaca* and the African *T. contorta* and *T. longiflora.* The usually more or less ellipsoid seeds are mostly embedded in a pulpy aril.

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APPENDIX: PLUMERIOIDEAE

Provisional incomplete survey of tribes, subtribes and genera, with number of species and parts of the world

1. *Carisseae*

   Couminae
   Parahancornia 6, Am.
   Couma 6, Am.

   Melodinae
   Melodinus ±45, As.

   Carissinae
   Carissa ±20, Afr., As.
   Acokanthera 5, Afr.

   Lacmelleinae
   Lacmellea ±15, Am.
   Hancornia 1, Am.

   Landolphiinae
   Landolphia 54, Afr.
   Chamaeclitandra 1, Afr.
   Clitandra 1, Afr.
   Orthopichonia 9, Afr.
   Anthoclitandra 2, Afr.
   Aphanostylis 3, Afr.
   Pacouria 2, Am.
   Dictyophleba 4, Afr.
   Vahadenia 2, Afr.
   Ancylobotrys 10, Afr.
   Saba 3, Afr.

   Willughbeiinae
   Cylindropsis 1, Afr.
   Willughbeia ±15, As.
   Urnularia 5, As.

   Leuconotidinae
   Bousigonia 2, As.
   Leuconotis 7, As.
   Cyclocotyla 1, Afr.

   Pleiocarpinae
   Picralima 1, Afr.
   Hunteria 10, Afr., As.
   Pleiocarpa 7, Afr.

2. *Chilocarpeae*
   Chilocarpus ±15, As.

3. *Ambelanieae*

   Ambelaniinae
   Ambelania 5, Am.

   Macoubeinae
   Macoubea 2, Am.

4. *Tabernaemontaneae*
   Voacanga 14, Afr., As.
   Tabernaemontana ±100, trop.
   Tabernanthe 1, Afr.
   Schizozygia 1, Afr.
   Carvalhoa 1, Afr.
   Callichila 7, Afr.
   Stemmadenia 17, Am.
   Crioceras 1, Afr.
   Calocrater 1, Afr.

5. *Plumerieae*

   Craspidosperminae
   Craspidospermum 1, Madag.
   Stephanostegia 3, Madag.
   Dyera 1, As.

   Plectaneiinae
   Kamettia 1, As.
   Gonioma 2, Afr.
   Strempelopsis 2, Am.
   Plectaneia 10, Madag.

   Alstoniinae
   Alstonia ±60, Afr., As.
   Tonduzia 1, Am.

   Aspidospermatinae
   Diplorhynchus 1, Afr.
   Pycnobotrya 1, Afr.
   Aspidosperma ±70, Am.
   Microplumeria 2, Am.
   Cufodontia 3, Am.
   Geissospermum 1, Am.

   Catharanthinae
   Rhazya 1, Mid. East
   Amsonia 19, Am., As.
   Catharanthus 6, Afr., As.
   Vinca 3, Eur., As.

   Haplophytinae
   Haplophyton 1, Am.

   Plumeriinae
   Mortoniella 1, Am.
   Plumeria 15, Am.

   Holarrheninae
   Holarrhena 4, Afr., As.
   Carruthersia 4, As.
   Spirolobium 1, As.

6. *Rauvolfieae*

   Rauvolfiinae
   Cabucala 16, Madag.
   Petchia 1, Ceylon
   Rauvolfia ±70, trop.
   Podochrosia 1, N. Caled.

   Alyxiinae
   Alyxia ±70, As.
   Lepinia 2, As.
   Lepiniopsis 2, As.

   Ochrosiinae
   Ochrosia ±25, Masc., As.

   Vallesiinae
   Vallesia 10, Am.
   Kopsia ±20, As.

   Condylocarpinae
   Rhipidia 1, Am.
   Condylocarpon ±10, Am.

   Anechitinae
   Anechites 1, Am.

7. *Allamandeae*
   Allamanda ±15, Am.

Bothalia 14, 3 & 4: 803–808 (1983)

The genus *Trematocarpus* (Sarcodiaceae, Rhodophyta) in southern Africa and the exclusion of *Sphaerococcus (Chondrus) scutellatus*

R. H. SIMONS*

ABSTRACT

Trematocarpus Kützing in southern Africa is found to comprise four taxa in three species: newly described is *T. fragilis* (Ag.) De Toni var. **divaricatus** Simons, var. nov. Two of the species, *T. flabellatus* (J. Ag.) De Toni and *T. affinis* (J. Ag.) De Toni are restored to independent specific rank after being regarded as synonyms of *T. scutellatus* (Her.) Searles. It is shown that *Sphaerococcus (Chondrus) scutellatus* Her., the basionym of *T. scutellatus* refers to a species of *Gigartina*, therefore a new combination *Gigartina* **scutellata** (Her.) Simons is made for this species which was formerly known as *G. fastigiata* J. Ag. and *G. scabiosa* (Kütz.) Papenf. *Trematocarpus elongatus* Kütz. is relegated to synonymy under *T. fragilis* var. *divaricatus*.

RÉSUMÉ

LE GENRE TREMATOCARPUS (SARCODIACEAE, RHODOPHYTA) EN AFRIQUE DE SUD ET EXCLUSION DE SPHAEROCOCCUS (CHONDRUS) SCUTELLATUS

Trematocarpus *Kützing comprend désormais en Afrique de Sud quatre taxa répartis en trois espèces:* T. fragilis *(Ag.) De Toni var.* **divaricatus** *Simons est nouvellement. Deux des espèces* T. flabellatus *(J. Ag.) De Toni et* T. affinis *(J. Ag.) De Toni, sont replacées chacune a un rang spécifique, après avoir été considérées comme synonymes de* T. scutellatus *(Her.) Searles. Il est démontré que* Sphaerococcus (Chondrus) scutellatus *Her., basionyme de* T. scutellatus, *se rapporte à une espèce de* Gigartina; *par conséquent, une nouvelle combinaison,* Gigartina **scutellata** *(Her.) Simons, est faite pour cette espèce qui était antérieurement connue sous les noms de* G. fastigiata *J. Ag. et* G. scabiosa *(Kütz.) Papenf.* Trematocarpus elongatus *Kütz. est placé en synonymie de* T. fragilis *var. divaricatus.*

Schmitz (1889) lectotypified *Trematocarpus* Kütz. by *T. dichotomus* Kütz. from the Peruvian coast, at the same time citing *Dicurella* J. Ag. as its synonym, but making no specific transfers from *Dicurella.* These were made in 1900 by De Toni. Three species from South Africa were then recognized, namely *T. fragilis* (Ag.) De Toni, *T. flabellatus* (J. Ag.) De Toni and *T. affinis* (J. Ag.) De Toni. Kylin (1932, 1956), however, reinstated *Dicurella* J. Ag. as a separate genus with *D. fragilis* (Ag.) J. Ag. as lectotype, on the grounds that the anatomical details differed. In his earlier publication, Kylin (1932) suggested that *D. flabellatus* J. Ag. and *D. affinis* J. Ag. were conspecific, a view confirmed by Papenfuss (1940), who combined them under *D. scutellata* (Her.) Papenf.

More recently, Searles (1969) supported Schmitz's concept of *Trematocarpus,* reintroducing *T. fragilis* (Ag.) De Toni. *T. flabellatus* and *T. affinis,* however, he identified with *T. scutellatus* (Her.) Searles, therefore following Papenfuss's precedent.

My studies have, however, convinced me that *T. flabellatus* (J. Ag.) De Toni and *T. affinis* (J. Ag.) De Toni do indeed have separate status and that *T. scutellatus* (Her.) Searles is attributable to another genus. I have found, too, that there are forms assignable to *Trematocarpus* that do not fit any of the published descriptions except, perhaps, that of *T. elongatus* Kütz., which was described (Kützing, 1868) as having come from the Pacific Ocean. I discovered the representative collections of *T. elongatus* in the Leiden Rijksherbarium (NBV) and these are Pappe specimens collected at the Cape of Good Hope. *T. elongatus* Kütz. is quite clearly identifiable with *T. fragilis* (Ag.) De Toni and more particularly with what I regard as a new variety of this species, and that I here describe as *T. fragilis* var. *divaricatus* Simons, var. nov. *Trematocarpus*, as interpreted by Searles (*l.c.*), is basically cellular in structure and the fusion-cell of the cystocarps forms a complex network. I have found that the South African representatives assigned to *Trematocarpus* have these characters and, although the internal cells of terminal portions of both *T. flabellatus* and *T. fragilis* var. *divaricatus* are somewhat loosely associated, they are more compacted than are those of *T. dichotomus* specimens I have seen. It is possible that a separation of *Dicurella* and *Trematocarpus* is justifiable, but I hesitate to do so without better evidence. Figs 1–4 illustrate structures of the respective South African taxa. Cystocarps are hemispherical with an ostiole making a minute apical pore.

The identity of *Sphaerococcus (Chondrus) scutellatus* Hering seemed to have been resolved by Papenfuss (1940) when he found a specimen bearing this name in Herbarium Hamburgense (HBG) (Fig. 5). Not only did the specimen bear Hering's name, but also a description in Hering's own hand, little different from that published (Hering, 1841; Krauss, 1846); two specimens were apparently present, one fertile the other sterile (Papenfuss, *l.c.*) as was inscribed by Hering on the sheet. The evidence for supposing that the original Hering specimen of *S. (C.) scutellatus* had been traced seemed therefore to be complete and irrefutable. Having established that the relevant plant was, in his opinion, a *Dicurella*

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and that it was to be equated with the later names *D. flabellata* J. Ag. and *D. affinis* J. Ag., Papenfuss relegated these to synonymy of *Dicurella scutellata* (Her.) Papenf. My own researches led me to distinguish once again between the two J. Agardh taxa, so that it became necessary for me to decide to which of the two the combination *D. scutellata* should be applied. This could only be resolved by seeing and examining the type of *D. scutellata* sensu Papenfuss. This I managed with the help of Dr. G. F. Papenfuss among others, but was disappointed to find only fragments of the relevant material. Nevertheless, I was able to ascertain that all the fragments were of a kind and probably came from the same plant, a tetrasporophyte, and that this plant is probably the same as that seen by Papenfuss, who described (*l.c.*) 'seriately divided tetrasporangia'. This was significant, because the inscription on the sheet included a reference to two specimens 'exempl. sterile et fructiferum'; and also to 'capsulis sphaericis'. The tetrasporangiferous specimen might easily be thought to be sterile, since there is no obvious evidence of fruiting, whereas a cystocarpiferous plant would not escape such notice, and it could well be carrying 'capsulis sphaericis' in the manner of so many Red Algae. I immediately suspected that the 'fruiting' specimen had been misplaced, but diligent searching on the part of the staff at HBG failed to produce it, and it must be accepted that the present sheet is incomplete. This would have no importance were it not for the fact that Barton (1896) identified the fruiting plant as *Gigartina fastigiata* J. Ag. In itself this is not enough to justify the view that the Hering mount contained two different taxa, but this opinion becomes undeniably weighted when Barton's (*l.c.*) statements are considered; she states unequivocally that the fruiting specimen = *G. fastigiata* J. Ag. is 'quite different' from the sterile one which has the 'whole interior filled with roundish, thick-walled cells'. Such an interior characterizes the specimen that Papenfuss saw ('the plant is entirely cellular') and the fragments of the plant now associated with the Hering specimen. Since the Hering description applies more appropriately to the missing fruiting specimen = *Gigartina fastigiata* J. Ag., especially with respect to the cystocarps with their scutellate ostioles, the epithet cannot justifiably be assigned to what Papenfuss and I recognize as belonging in *Dicurella* J. Ag. On the contrary, *G. fastigiata* J. Ag. and *G. scutellata* (Hering) Simons are to be regarded as synonyms; the Hering name is the earlier and therefore becomes the correct name for the taxon. This combination replaces *G. scabiosa* (Kütz.) Papenf., which substituted for *G. fastigiata* J. Ag., an illegitimate later homonym.

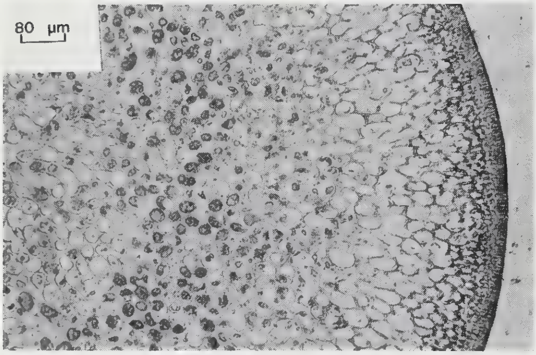

FIG. 1. — *Trematocarpus fragilis* var. *fragilis*. T. S. through a mature portion of an axis.

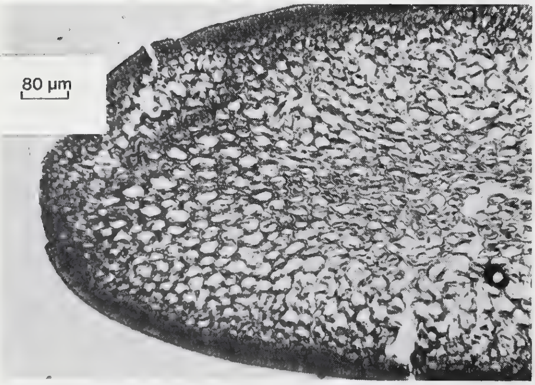

FIG. 2. — *Trematocarpus fragilis* var. *divaricatus* T. S. through a mature portion of an axis.

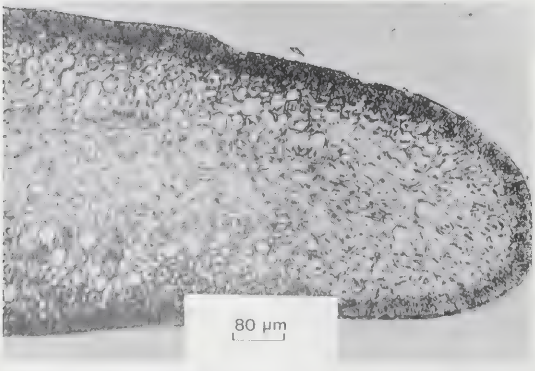

FIG. 3. — *Trematocarpus flabellatus*. T. S. through a mature portion of an axis (*Simons* 5245)

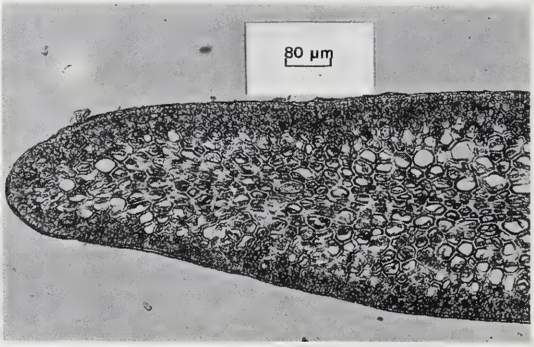

FIG. 4. — *Trematocarpus affinis*. T. S. through a mature portion of an axis.

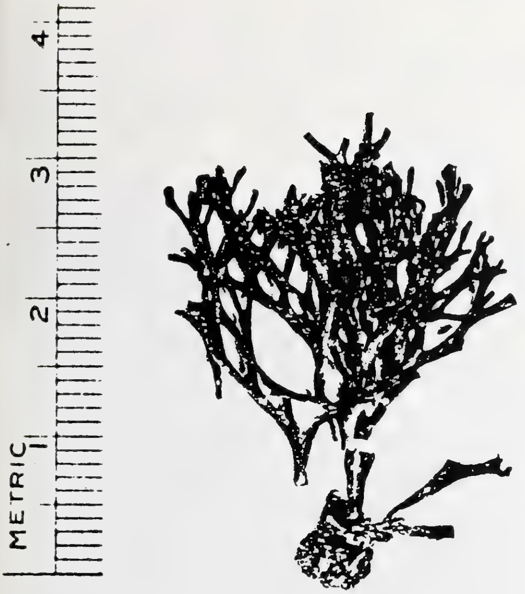

FIG. 5. — *Dicurella scutellata.* 'Type' of *Sphaerococcus (Chondrus) scutellatus* Hering in Herb. Hamburg: copy of a photograph of the sterile plant fragments associated with the Hering MS description of *S. (C.) scutellatus* as seen by Dr G. F. Papenfuss and referred to in his paper (Papenfuss, 1940).

Gigartina scutellata *(Her.) Simons,* comb. nov.

Sphaerococcus (Chondrus) scutellatus Hering in Ann. Mag. Nat. Hist. 8: 91 (1841); Krauss (as *Chondrus scutellatus)* in Flora, Regensb. 29: 210 (1846); non Kützing, Sp. Alg.: 736 (1849); Tab. Phyc. 17: 16, t. 56 (1867) = *Polyopes constrictus* (Turn.) J. Ag. Neotype: Cape, 3217 (Vredenburg): Klein Paternoster Bay (−DD), *Simons 452* (Seaweed Research Unit, Sea Fisheries Institute, Department of Agriculture and Fisheries, Cape Town).

Gigartina fastigiata J. Ag. in Vet.-Akad. Handl. 6: 86 (1850; dated 1849); Sp. Alg. 2: 276 (1851); Sp. Alg. 3: 193 (1876); non Postels et Rupr. (1840).

Chondrus scabiosus Kütz., Tab. Phyc. 17: 19,t. 63a−b (1867); *Gigartina scabiosa* (Kütz.) Papenf. in Jl S. Afr. Bot. 9: 88 (1943).

This species is a common constituent of the intertidal flora of the whole Benguela System that washes the west coast of the Cape Province of South Africa. Its dichotomously branched axes present a similar appearance to those of *Trematocarpus*, but they are generally more fleshy in the fresh state, and either a deeper purple or a brownish-yellow.

Trematocarpus fragilis *(Ag.) De Toni,* Syll. Alg. 4: 417 (1900); Searles in Phycologia 8: 26 (1969). Lectotype: Cap. bon. Spei (Cape Province, South Africa), *De La Lande* s.n. sub Agardh Herb. No. 28674 (LD).

Tufts of many erect wiry fronds up to 300 mm high, emerging from a disciform holdfast; *fronds* scarcely branched in the lower half, thereafter dichotomising subflabellately at progressively shorter intervals and attenuated to bluntly rounded or subacute tips.

Two varieties are here distinguished for the first time.

(a) var. **fragilis**

Sphaerococcus fragilis Ag., Sp. Alg. 1: 253 (1824). *Dicurella fragilis* (Ag.) J. Ag., Sp. Alg. 2: 630 (1852); Sp. Alg. 3: 406 (1876); Searles in Univ. Calif. Publ. Bot. 43: 69 (1968). *Chondrus fragilis* (Ag.) Grev., Alg. Brit. 55 (1839); Kütz., Sp. Alg.: 738 (1849).

Gigartina flabellata Kütz., Sp. Alg.: 751 (1849); Tab. Phyc. 18: 2, t. 5 (1868).

Dicurella elatior Harv., Ner. Austr. t. 50 (1847). nom. nud.

Specimens incorrectly determined: *Ahnfeltia elongata* Kütz. in Herb. NBV sub Herb. Lugd. Bat. 939,6. . .100; ibid. as *Dicurella scutellata* (Her.) Papenf.; *Gelidium fastigatum* Kütz.: Hohenacker 1860 sub Herb. Lugd. Bat. 938,334. . .141 (non Hohenacker 475a 1860 and 475a.c. sub Herb. Lugd. Bat. 938,334. . .143 = *Trematocarpus flabellatus* (J. Ag.) De Toni).

This variety (Fig. 6) has long axes, up to 300 mm, that are fairly rigid and branched in the distal half only. Branching is dichotomous-subflabellate with internodes becoming progressively shorter distally. The axils are more or less rounded and the ultimate segments look like the prongs of a hay-fork, that is, widely divergent at first, then becoming more or less parallel. The often entirely terete axes may in some specimens be somewhat compressed, but there is always a terete stipe and the ultimate segments are little, if at all, compressed.

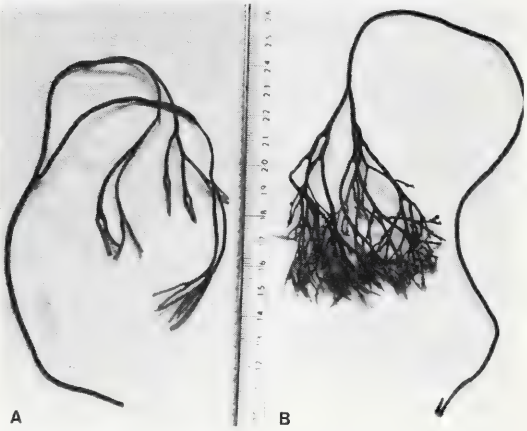

FIG. 6. — *Trematocarpus fragilis* var. *fragilis.* Whole plants: A, non-cystocarpiferous; B, cystocarpiferous.

The epidermal layer consists almost always of more or less cylindrical cells, with the long axes vertical to the surface, and up to four times longer than wide. Although entirely cellular (in transverse section), there is tissue differentiation into epidermis, outer cortex, inner cortex and medulla. The medulla can, when axes are terete, occupy up to half the sectional area, and consists of cells markedly variable in cross-sectional shape, but they are generally smaller than those surrounding them. The outer cortex contains two or three rows of roughly isodiametric cells, inside which is an inner cortex filled with coffin shaped cells whose long axes are at

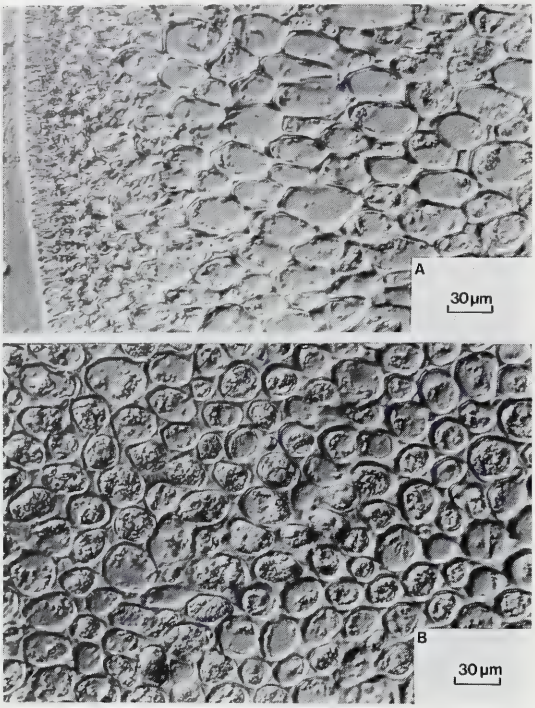

FIG. 7. — *Trematocarpus fragilis* var. *fragilis*. T. S. of mature portion of an axis: A, outer tissues; B, inner core.

right-angles to the surface. Fig. 7A & B show the various tissues.

Cystocarpiferous plants are often remarkable for their more slender distal segments so that the cystocarps, which in any case are rather prominent, appear disproportionately large. Tetrasporangia occur in pseudonemathecia that more or less cover terminal and subterminal segments.

This is mainly sublittoral but, not infrequently, it grows in tidal pools in the lower reaches of the littoral zone. It is characteristic of the Benguela System on the west coast of southern Africa and does not, as far as I know, reach east of Cape Agulhas. There is a record, via Suhr (1834), of *Halymenia furcellata* var. *cartilaginea* (= *Dicurella fragilis,* fide J. Agardh, 1852) from Algoa Bay (= Port Elizabeth), a locality well east of Cape Agulhas; unlike J. Agardh, I am of the opinion that the plant in question is *Trematocarpus flabellatus,* because, not only does Port Elizabeth lie beyond the known range of the plant but the illustration by Suhr (*l.c.*, t. 22, f. 16) shows what looks like a sorus typical of *T. flabellatus* (*q.v.*), a species known to occur as far east as Port Elizabeth. I have, therefore, excluded *Halymenia furcellata* var. *cartilaginea* Suhr from the synonymy of *T. fragilis* and placed it with *T. flabellatus.*

(b) var. **divaricatus** *Simons* var. nov., a typo thallo suo complanato, saepe ad apices submembranaceo et contorto, ramis divergentibus, differt. (Fig. 8).

TYPE.— Cape, 3318 (Cape Town): Oudekraal (= Hottentotshuisie) (−CD), *Jarman s.n. sub Simons 4994* (Seaweed Research Unit, Sea Fisheries Institute, Department of Agriculture and Fisheries, Cape Town).

T. elongatus Kütz., Tab. Phyc. 18: 2, t. 4d-g (1868); Searles in Phycologia 8: 26 (1969).

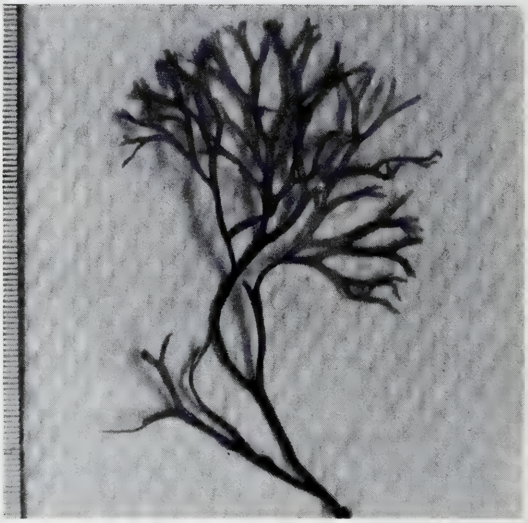

FIG. 8. — *Trematocarpus fragilis* var. *divaricatus* var. nov. Portion of a tuft sharing the same discoid holdfast.

The most remarkable differences between this variety and the typical variety are the flattened thallus and divergent forking at dichotomies, a characteristic that is not invariable. One or two branchings frequently occur in the proximal half. I have seen and collected many examples of this variety at Bakoven just a kilometre or two north of Hottentotshuisie. It seems always to be submerged at least 2 m below mean sea level. Anatomically there are slight differences between the two varieties such as the rather laxer tissues of var. *divaricatus* in the ultimate segments, but these are less obvious when comparing the respective female vegetative tissues; the pericarps making up the protective walls of cystocarps, however, seem to be distinguishable. Fig. 2 shows the main feature of the mature tissue-disposition of this variety.

The two taxa that Papenfuss (1940) sank under *Dicurella scutellata* (= *Trematocarpus scutellatus* sensu Searles), namely *D. flabellata* and *D. affinis*, are in fact distinguished from each other in the features detailed by J. Agardh (1852 and elsewhere). The differences are more subtle than they are obvious: branching in both is dichotomous in one plane and the plants are much the same height. *T. flabellatus*, though, is dorsiventral (Fig. 9) against the bilateral symmetry of *T. affinis* (Fig. 10): not only is this true of the vegetative axes, but it applies also to the distribution of the sori, both male and tetrasporangial. In *T. flabellatus* the segments are plano-convex in section and the sori confined to the plane surface, whereas in *T. affinis* sori discontinu-

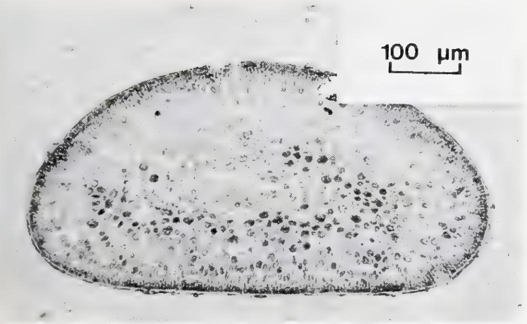

FIG. 9. — *Trematocarpus flabellatus.* T. S. through terminal segment showing plano-convex character of the thallus.

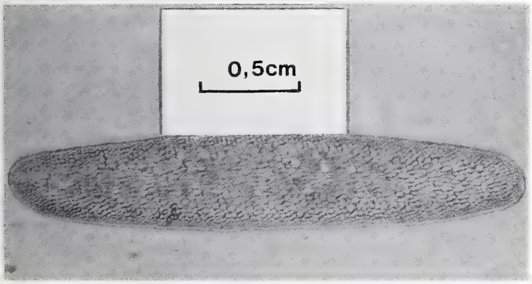

FIG. 10. — *Trematocarpus affinis.* T. S. through terminal segment showing bilateral character of the thallus.

ously coat the surface of fertile segments usually causing some distortion of the affected parts.

Trematocarpus flabellatus *(J. Ag.) De Toni,* Syll. Alg. 4: 418 (1900). Lectotype: Cape, 3318 (Cape Town); Sea Point (−CD), *Harvey s.n. sub Agardh Herbarium Nos. 28689* (Fig. 11) *& 28690* as *Dicurella flabellata* J. Ag.

Phyllotylus flabellatus J. Ag. in Vet. -Akad. Öfvers. 4: 9 (1847). *Dicurella flabellata* Harv. t. 50 (1847). nom. nud., J. Ag., Sp. Alg. 2: 632 (1852); J. Ag., Sp. Alg. 3: 407 (1876).

Halymenia furcellata var. *cartilaginea* Suhr in Flora 17: 733 (1834).

Trematocarpus polychotomus Kütz., Sp. Alg.: 785 (1849); Tab. Phyc. 19: 27, t. 73 (1869).

Gelidium fastigatum Kütz., Tab. Phyc. 18: 21, t. 61a−b (1868).

Dicurella scutellata Papenf. (1940), in part; *Trematocarpus scutellatus* Searles (1968), in part.

This species commonly occurs in tidal pools forming low-growing (up to 80 mm, rarely more) magenta-coloured compound fan-like tufts that are distinctive and very pretty. The fans are slightly retrorse. Although more typically a Benguela System (i.e. west coast) species, some collections have come from as far east as Port Elizabeth.

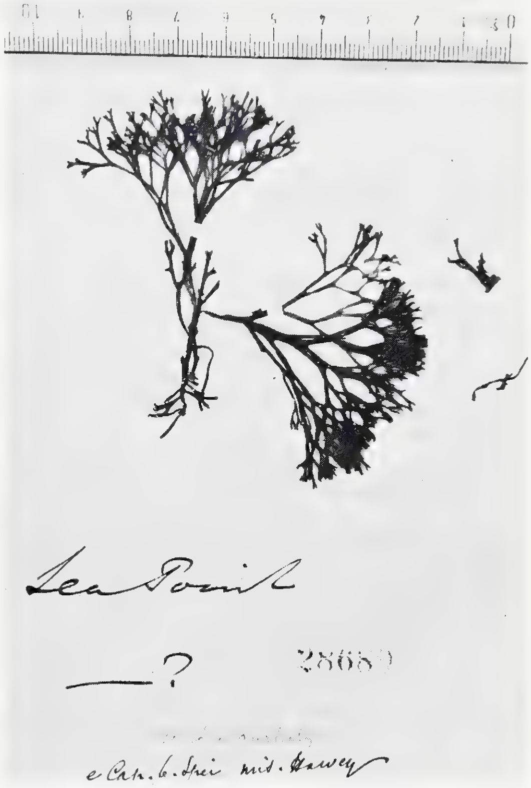

FIG. 11. — *Trematocarpus flabellatus. Agardh Herb.* No. 28689 in Lund. Herb. (LD) — part of type material.

Ultimate segments of the axes are subspatulate (Fig. 12) with a convex surface often on the dorsal side, i.e. back of the upward-facing surfaces of the slightly arched lobes of the fan. The other surface is either plane (Fig. 9) or very little concave. The linear sori make a raised pad of tissue on the non-convex surface, disposed in such a manner as to leave a sterile surround at the margins. Only the most distal segments are involved. Male sori are yellowish and, therefore, distinctive.

Epidermal cells are usually cylindrical, being anticlinally elongated. The central tissue is composed of more or less large, and angled cells in which there may be a core of distinctly smaller cells buried in a thick matrix (Fig. 3).

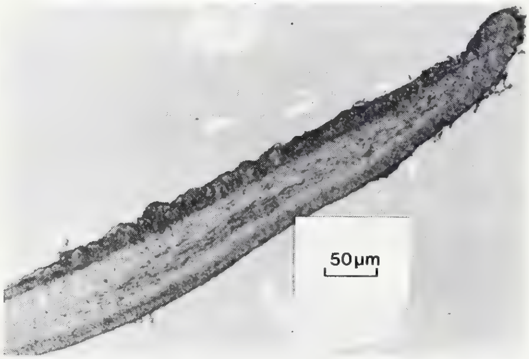

FIG. 12. — *Trematocarpus flabellatus. Agardh. Herb.* No. 28690 in Lund. Herb. (LD) — part of type material. L. S. through a terminal segment that is tetrasporiferous. Note subspatulate character, and sorus on one surface only.

I have found anomalous forms, some with sori containing only undivided sporangia (?monosporangia) that suggest immature tetrasporangia and others with parts having morphological and anatomical features similar to those of *T. affinis*. Monospores are not unusual features of many Red Algae and these are variously interpreted. In this instance, their production is sometimes associated with the vegetative anomalies mentioned above. I consider these forms to be hybrids involving *T. flabellatus* and *T. affinis* as parents.

Trematocarpus affinis *(J. Ag.) De Toni* Syll. Alg. 4: 419 (1900). Type: Cap. bon. Spei (= Cape Province, South Africa). *Pappe* sub Agardh Herb No. 28695 (as *Phyllotylus affinis* J. Ag.) LD; authenticated representative material: *Phyllotylus affinis* J. Ag. 25. CBS Tabelbay in Herb. Binder (HBG) (vid. J. Ag., Sp. Alg. 2: 632, 1852).

Dicurella affinis J. Ag., Sp. Alg. 2: 632 (1852); Sp. Alg. 3: 407 (1876). *Phyllotylus affinis* J. Ag. ms. in Herb. LD & HBG, nom. nud.

Dicurella scutellata Papenf. (1940) in part and the specimen associated with the ms. name of *Chondrus scutellatus/Sphaerococcus* in Herb. HBG; Searles (1968), in part; *Trematocarpus scutellatus* Searles (1969), in part.

This species is quite a frequent constituent in samples of seaweeds dived out in Cape west coast waters as much as 15 m deep. It does, however, approach the intertidal zone, where, I think, a certain amount of natural crossing with *T. flabellatus* takes place. Its general appearance is very similar to that of *T. flabellatus*. Its naviculoid cross-sections (Fig. 10) and its tissue-construction and distribution, nevertheless, distinguish it from that species: epidermal cells are often cuboid (Fig. 13A), whereas the medulla occurs as scarcely more than a median plate of flattened cells (Fig. 13B); cortex consists of more or less isodiametric round-angled cells that may become slightly flattened parallel with the surface; sori more or less surround terminal and subterminal segments and their uneven distribution leads to some superficial distortion.

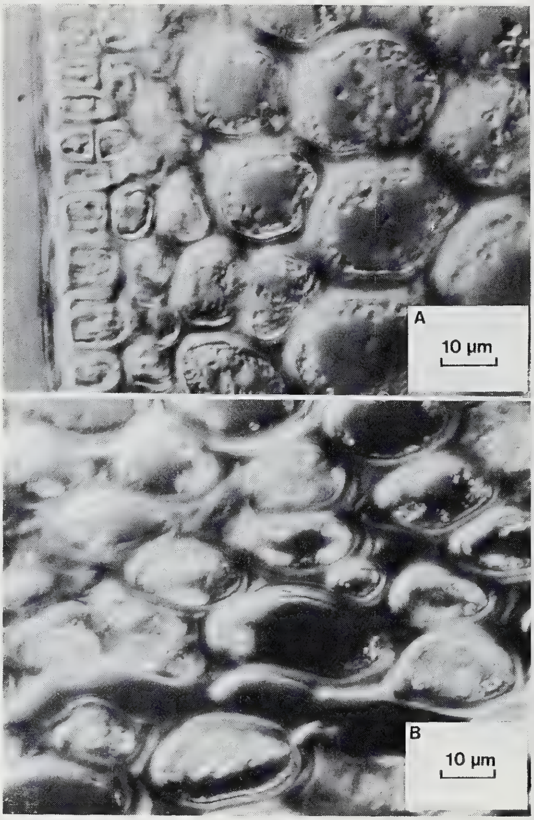

FIG. 13. — *Trematocarpus affinis*. T. S. of terminal segment: A, outer tissues; B, core tissue — cells are flattened in the plane of flattening of the thallus.

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I am especially grateful to the Management of the Fisheries Development Corporation whose funding enabled me to visit Lund in Sweden, Leiden in Holland and Hamburg in Germany. In each of these places I was given every aid to further my studies and I want to thank the respective curators and their staffs for their painstaking assistance. The University of Cape Town and more especially the successive Heads of the Botany Department earn special mention because of their generous accommodation of the Seaweed Research Unit of the Sea Fisheries Institute since its inauguration in 1956.

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Anatomy of the genus *Kyllinga* in South Africa

F. M. GETLIFFE NORRIS*

ABSTRACT

The anatomy of underground and aerial parts of South African species of the genus *Kyllinga* Rottb. is described. SEM micrographs of stomata and of silica bodies are provided. Two new records for South Africa: *K. polyphylla* Willd. ex Kunth and *K. nemoralis* (Forst.) Dandy are included.

RÉSUMÉ

ANATOMIE DU GENRE KYLLINGA *D'AFRIQUE DU SUD*

L'anatomie des parties souterraines et aériennes d'espèces Sud-Africaines du genre Kyllinga *Rottb. est décrite. Des photographies au MEB des stomates et des corps siliceux sont présentées. Deux espèces nouvelles pour l'Afrique du Sud,* K. polyphylla *Willd. ex Kunth et* K. nemoralis *(Forst.) Dandy, sont comprises dans cette étude.*

INTRODUCTION

Interest in the anatomy of Cyperaceae as a source of taxonomic data has been stimulated by the review by Metcalfe (1971) of the family, the discovery of the Kranz syndrome in the family and speculation that it has evolved twice in the Cyperaceae (Raynal, 1973), and with two anatomical manifestations (Laetsch, 1971; Carolin 1977).

Kyllinga has been included in two accounts of general anatomical features (Metcalfe *l.c.* and Govindarajalu, 1969) and mentioned in discussions of the Kranz syndrome by Brown (1975). Not all the South African species have, however, been surveyed.

MATERIALS AND METHODS

At least one example of each species represented in Natal was examined and, where possible, comparisons of other populations were made. A selected list of specimens is provided in Appendix 1.

Hand sections of aerial parts were cleared in saturated solution of chloral hydrate, washed and stained in Delafield's Haematoxylin before mounting in safranin jelly. Leaves, sheaths, culms and bracts were sectioned in the upper portion of the lower third of the organ where maximum size and maturity occurred.

Roots were sectioned 4–6 mm behind the growing points and rhizomes at an internode near the growing tip. Stolons were sectioned midway between plants. Underground portions were embedded in paraffin wax and sectioned with a rotary microtome; stained in safranin and fast green and mounted in Canada Balsam. Preliminary studies of the epidermis at light microscope level were made by stripping the epidermis using Metcalfe's method (1960) of scraping away underlying tissues. Silica bodies were studied by mounting epidermal strips in a saturated aqueous phenol solution.

For SEM studies, the epidermides were prepared by the method recommended by Stant (1973). Preparations of silica from vegetative parts were made by digesting the organic material in hydrogen peroxide and perchloric acid (Breveden & Hodges, 1973), after washing, the silica remnants were mounted on stubs and coated with gold palladium for viewing on a JS100 microscope.

RESULTS

Underground organs

Neither Metcalfe (1971) nor Govindarajalu (1969) distinguished between the rhizome of species such as *K. melanosperma* Nees and the stolon of *K. pulchella* Kunth or *K. nemoralis* (Forst.) Dandy. Both authors, however, drew attention to two anatomical patterns which correlate with this distinction.

Rhizome

Though morphologically variable in that internodes may be short *(K. melanosperma)* or long (*K. intricata* Nees and *K. colorata* (L.) Druce), anatomically there was a common pattern (Fig. 1).

In transverse section, the rhizome was found to consist of a prominent central stele separated from the cortex by a well defined endodermoid layer of radially elongated cells conspicuously lignified (Fig. 2B).

Amphivasal bundles were closely scattered within the parenchymatous ground tissue of the stele and concentrated particularly towards the periphery. Occasional cells of the ground tissue were filled with tannin.

Each vascular bundle consisted of a small central mass of sieve tubes and companion cells (particularly clear in *K. polyphylla*) surrounded by a single ring of xylem vessels and tracheids. The vessels were small in diameter (Fig. 2C). This amphivasal structure of the bundle is characteristic of the groups of Cyperaceae assigned to the Amphivasae by Plowman (1906).

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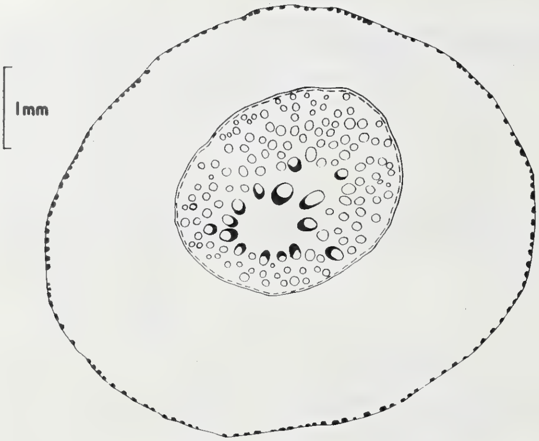

FIG. 1.—Plan of distribution of tissues in transverse section of rhizome of *Kyllinga polyphylla* Willd. ex Kunth.

A sheath of sclerenchyma cells which Plowman (*l.c.*) called the bundle periderm, surrounded most vascular bundles. Occasionally this was not clearly defined, whereas the bundle periderm of the more central bundles was often exaggerated centripetally, e.g. *K. polyphylla.*

Between the vascular bundles and endodermoid layer was a layer of thickened cells which varied from species to species. In *K. erecta* Schum. it consisted of 1–2 layers of sclerenchyma often merging into the bundle periderm of the peripheral bundles while in the majority of species investigated, it consisted of a single outer layer of sclerenchyma associated with 2 or 3 inner layers of small parenchyma cells which may later become lignified (Fig. 2B).

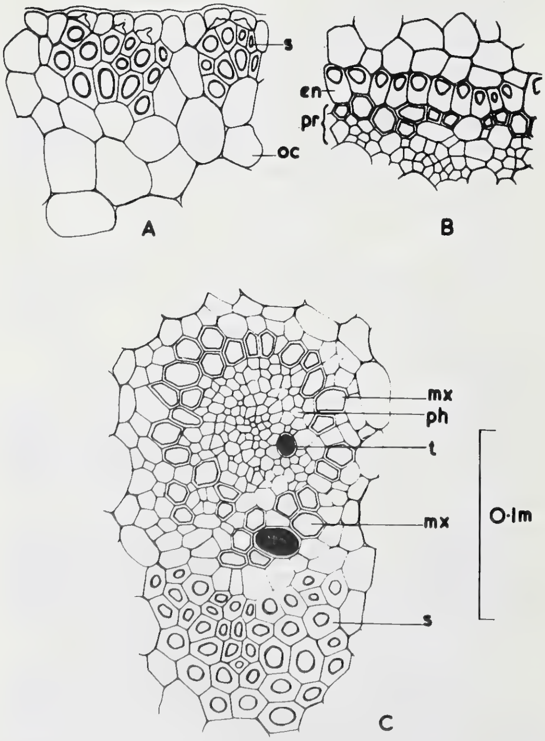

FIG. 2.—Details of portions of transverse sections of rhizome of *Kyllinga polyphylla* Willd. ex Kunth. A, epidermis and outer cortex (oc) with hypodermal strand (s); B, endodermoid layer (en); C, vascular bundle. (metaxylem, mx; phloem, ph; tannin cell, t; sclerenchyma, s.)

The cortex, too, varied. Probably, in all species, the cortex of the young rhizome is a simple starch-bearing parenchymatous zone which may change as the rhizome matures. In *K. polyphylla* and *K. erecta* the cortex retained this compact uniform form, but in *K. elatior* Kunth and *K. melanosperma,* the outer zone of the cortex became slightly lignified. Three collections of *K. pauciflora* Ridl. (*Getliffe* 174, 224, 265) and one of *K. colorata* (*Getliffe* 191) possessed an aerenchymatous inner cortex which was particularly noticeable in the ventral portion of the rhizome adpressed to the soil. All these plants grew in damp situations. Two other populations of *K. colorata (Getliffe* 23, *Ross* 993*)* growing in less damp habitats, did not develop this aerenchyma.

An irregular ring of groups of small sclerenchyma cells formed a type of hypodermis or series of hypodermal ribs within the epidermis of *K. erecta* and *K. polyphylla* and the epidermal cells of these two species contained small 'pegs' of lignin. A single tooth-like peg of lignin protruded from the inner tangential wall of each cell and extended about halfway into the cell (see Fig. 2A). A single epidermis of thickwalled cells surrounded other rhizomes examined.

Stolon

The stolons of *K. pulchella* and *K. nemoralis* consisted of a narrow stele and an aerenchymatous cortex (Fig. 3A).

The bundles of the stele were closely packed peripherally making it difficult to distinguish individual bundles. Centrally, they became more widely separated. Bundles were frequently U-shaped as the xylem did not completely surround the phloem (see Fig. 3C). True amphivasal bundles were rare even in the older portions of the more robust stolons of *K. nemoralis.*

In *K. pulchella* the endodermoid layer comprised a few layers of fairly large hexagonal, slightly lignified cells, whereas in *K. nemoralis* it was difficult to distinguish the thickened endodermoid layer from the thickened inner cortical layers.

In both species, an aerenchymatous inner cortex was differentiated from a narrow parenchymatous outer cortex. The aerenchyma was particularly well developed in *K. nemoralis* collected from a damp sandy river bed. Hypodermal ribs similar to those found in rhizomes were present and a simple epidermis enclosed the stolons.

Fresh material of *K. albiceps* (Ridl.) Rendle was not available for study.

Root

The young root consisted of a very narrow polyarch stele and a broad cortex of radially

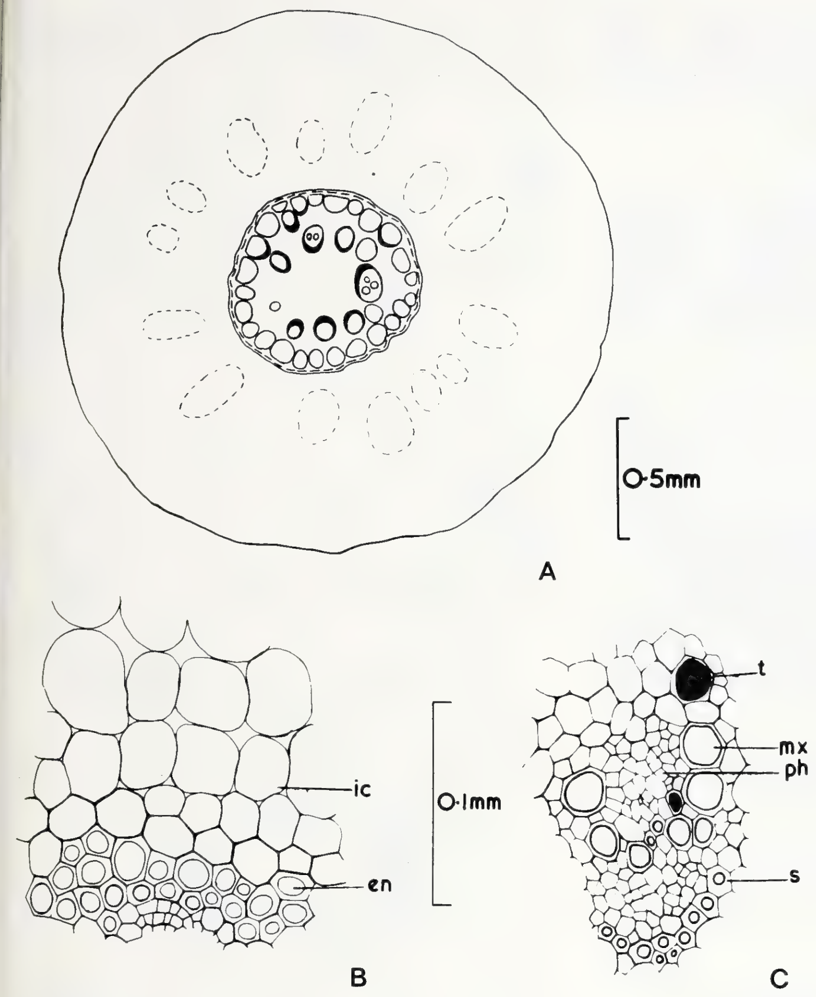

FIG. 3.—Stolon of *Kyllinga nemoralis* (Forst.) Dandy in transverse section. A, plan of distribution of tissues; B, inner cortex (ic), endodermoid layer (en); C, vascular bundle in detail. (tannin cell, t; metaxylem vessel, mx; phloem sieve tube, ph; sclerenchyma, s.)

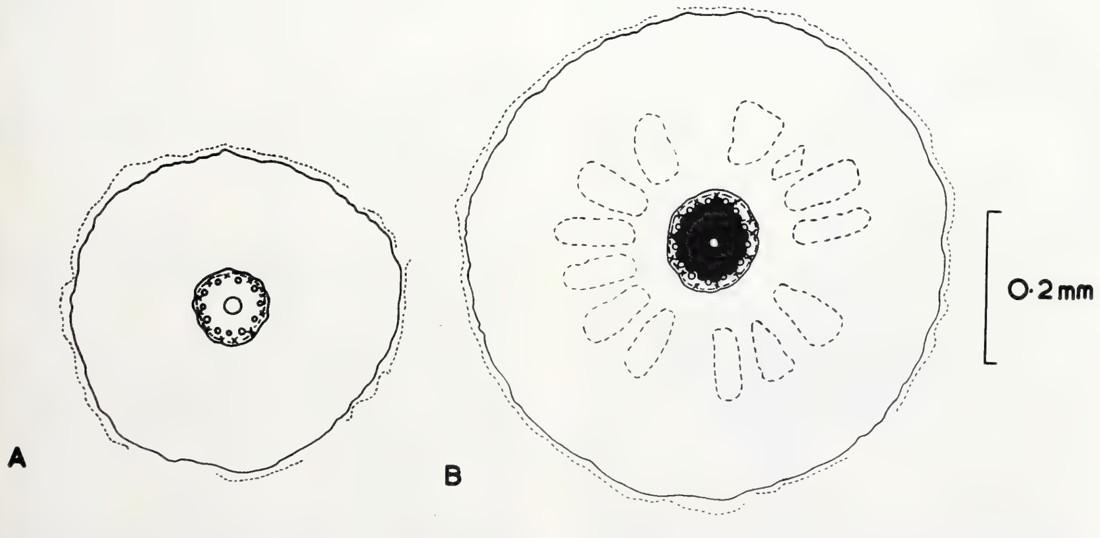

FIG. 4.—Plan of distribution of tissues in roots. A, young root of *Kyllinga nemoralis* (Forst.) Dandy; B, older root of *K. pauciflora* Ridl. with aerenchymatous cortex.

arranged, starch-filled parenchyma cells. The cortex was frequently differentiated into an inner slightly thickened cortex and an outer cortex of which the outer layers were also slightly thickened and closely packed forming an exodermis beneath the piliferous layer (Fig. 4).

In older roots, aerenchymatous tissue developed in the inner cortex due to partial breakdown of radial rows of cortical parenchyma. This aerenchyma was frequently very extensive and made sectioning difficult as the complete cortex became detached from the stele, or the piliferous layer and exodermis from the remainder of the cortex.

Centrally placed in the stele were from 1–5 large metaxylem vessels in a ground tissue of tracheids and sclerenchyma. With age, this packing tissue became heavily lignified. Alternating groups of phloem and protoxylem were arranged peripherally. From 8–22 groups of phloem, each composed of 1–4 sieve tubes with companion cells were found. Protoxylem groups usually consisted of a single small vessel associated with, perhaps, 1 or 2 tracheids.

The protoxylem vessels interrupted the pericycle of hexagonal slightly lignified cells. Enclosing the stele was a well defined endodermis of large, radially elongate elements lignified on the inner tangential and radial walls (Fig. 5).

Aerial parts

Leaf sheath

In transverse sections, the sheath was a complete triangle (Fig. 6B). Two sides were better developed than the third, and were continuous with the blade. The intersection of these two sides formed the keel with a prominent vascular bundle which extended into the main vein of the leaf. The leaves, and therefore the sheaths, have 1/3 phyllotaxy.

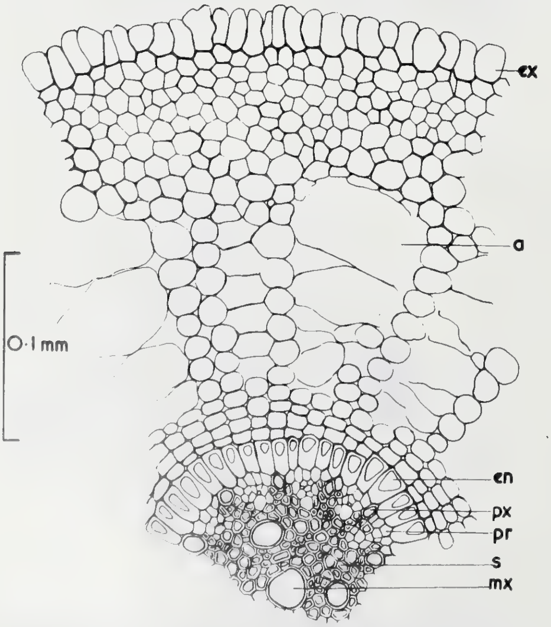

FIG. 5.—Detail of portion of transverse section older root of *Kyllinga pauciflora* Ridl. (ex = exodermis; a= airspace; en = endodermis; pr = pericycle; px = protoxylem; mx = metaxylem vessel; s = sclerenchyma.).

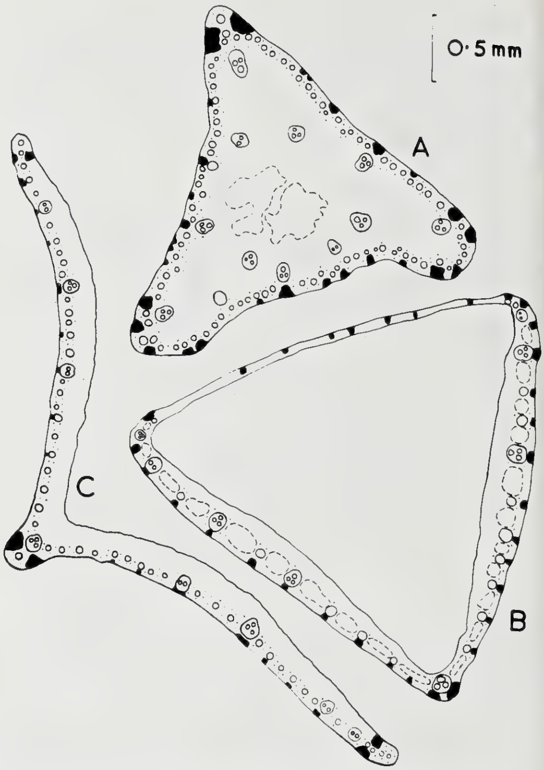

FIG. 6.—Plan of distribution of tissues in transverse section of leaf culm and leaf sheath of *Kyllinga nemoralis* (Forst.) Dandy.

The broad arms of the sheaths contained many vascular bundles alternating with well developed airspaces (Fig. 6B), whereas the third side was 2–3 cells thick, without vascular strands but with small hypodermal strands of sclerenchyma. The vascular bundle of the keel was solitary, but a first order bundle of the type found in the midrib of the leaf and subtended by two pulviniform sclerenchyma strands. Similar smaller strands were associated with minor vascular bundles. Stomata were found on the outer epidermis and the inner epidermis was composed of small thinwalled cells.

Leaf

In transverse section the leaves of *Kyllinga* species were V-shaped (Fig. 6C) or, in the case of the broad leaves of *K. elatior,* flanged V-shaped (terminology after Metcalfe, 1971).

Up to 88 vascular bundles were present in the transverse sections of these. The larger midrib bundle and two or three of the bundles of the blade were large first order bundles with two prominent metaxylem vessels, whereas the rest were smaller second order bundles without conspicuous vessels.

Metcalfe (1971) drew attention to the two superimposed bundles of the midrib of *Kyllinga* and *Pycreus* species as distinct from other members of the Cypereae. His material of *K. erecta* was an exception, but in the material of *K. erecta* examined in this study, two bundles were found in the midrib but *K. pulchella* leaves had one. This may, however, not be a consistent feature of *K. pulchella* which may vary as does *K. erecta.*

The upper vascular bundle of a double bundle midrib is a large first order bundle with two prominent metaxylem vessels. The lower vascular bundle is very much smaller. Associated with the midrib vascular tissue is the pair of pulviniform sclerenchyma girders characteristic of the Cypereae (Metcalfe, 1971) (Fig. 7A).

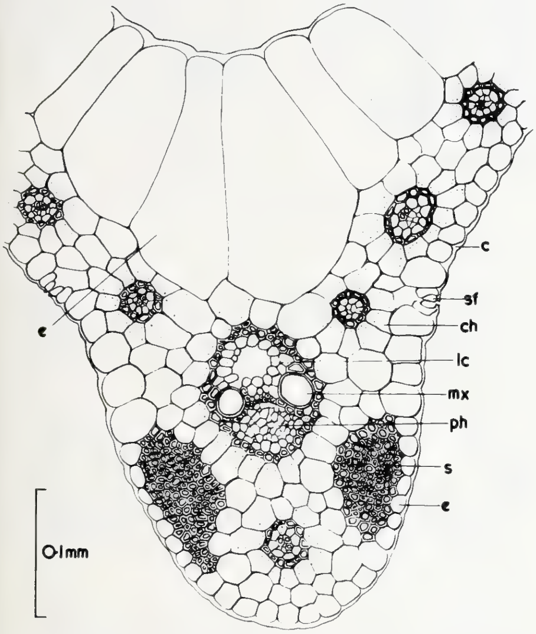

FIG. 7.—Detail of transverse section of midrib of *Kyllinga nemoralis* (Forst.) Dandy. (e = epidermis; c = cuticle; st = stoma; ch = chlorenchyma; lc = lysigenous cavity; mx =metaxylem vessel; ph = phloem; s = sclerenchyma.).

The vascular bundles of *Kyllinga* are surrounded by a conspicuous inner sheath, the Kranz sheath, and an outer sclerenchymatous sheath. Radiating chlorenchyma of the mesophyll is particularly conspicuous around the smaller bundles (Fig. 8). In the larger bundles, the inner Kranz sheath is interrupted by the two metaxylem vessels but in smaller bundles is a complete ring in transverse section. The inner sheath cells have been shown to have the modified chloroplasts of the Kranz syndrome (Carolin, 1977; Gordon-Gray & Gilliland, 1978) in contrast to the Calvin type chloroplasts of the radiating mesophyll cells (Laetsch, 1969).

This pattern of inner Kranz sheath and outer sclerenchymatous sheath is characteristic of the Chlorocypereae and is contrasted with the fimbristyloid type in which an additional outer sheath later is present.

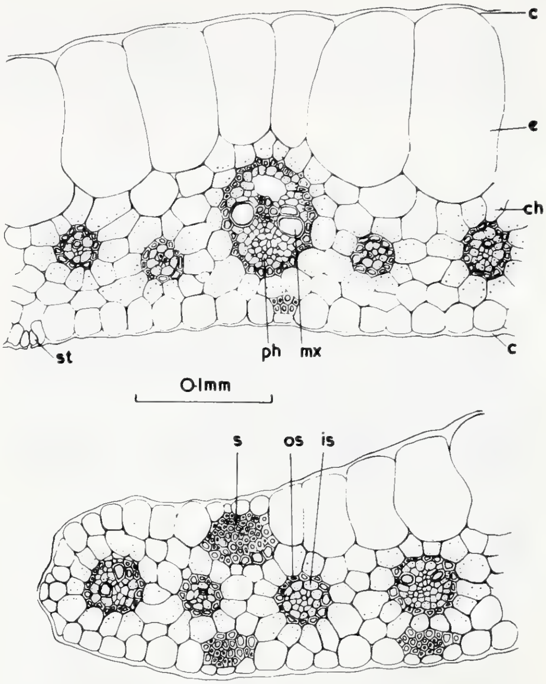

FIG. 8.—Detail of portions of transverse section of blade of leaf of *Kyllinga nemoralis* (Forst.) Dandy. A, median portion of blade (c = cuticle; e = epidermis; ch = chlorenchyma sheath; mx = metaxylem; ph = phloem; st = stoma.); B, lip of blade. (s = sclerenchyma; os = outer sclerenchymatous bundle sheath; is = inner sclerenchymatous bundle sheath.)

The most conspicuous feature of the leaves was the upper epidermis of large elongated cells occupying half the width of the leaf cross sections. In most leaves, the epidermis was a single layer of cells, but in some examples of *K. alba* (*Ross* 693) and *K. alata* Nees (*Ward* 4980, *Lennox* s.n.), it consisted of a double row of smaller cells. In several sections of *K. alata* (*Getliffe* 169, *Ward* 554) a double epidermis at the margins gave way to a single epidermis above the midrib. Further study of this feature is necessary to establish whether the number of rows of epidermal cells is arbitrary or governed by environmental factors, such as available moisture.

In every case, the upper epidermis was covered by a thick cuticle and was without stomata. Occasional hypodermal ribs of sclerenchyma occurred beneath this epidermis, but in none of the species examined was this very conspicuous except at tips of the leaf (Fig. 8B). The lower epidermis, which consisted of small rounded cells covered by a thin cuticle, was well provided with stomata. Beneath this layer, small hypodermal rib strands were frequent. In every case, silica bodies were restricted to epidermal cells adjacent to these strands. Air cavities between the vascular bundles were mentioned by Metcalfe (*l.c.*), but appear to be very rare in the genus and were seen only in *K. polyphylla* in this study.

Bracts

The anatomy of the bracts resembled that of the leaf in every respect except that they were smaller and graded in size from lowest to smallest upper bract.

Culms

The culms of all *Kyllinga* species investigated were basically triangular in transverse section (Fig. 9). Variation from the concave-sided, acute-angled triangle of *K. elatior* to the rounded triangle of *K. pulchella* and *K. alata* was found. The shape in transverse section was more or less constant for each species with slight variations in the number of ridges and furrows in *K. odorata* (Fig. 9H). In the extreme variations such as *K. elatior* (Fig. 9A) and *K. pauciflora* (Fig. 9I), the shapes were sufficiently distinctive to be considered as diagnostic characters. Culms of *K. nemoralis* (Fig. 9B), *K. polyphylla* (Fig. 9I), the shapes were sufficiently distinctive to be considered as diagnostic characters. Culms of *K. nemoralis* (Fig. 9B), *K. polyphylla* (Fig. 9F) and *K. melanosperma* (Fig. 9D), were all of similar shape and hardly distinguishable on this basis. Similarly, *K. colorata* (Fig. 9C) and *K. odorata* (Fig. 9H) were scarcely separable.

An epidermis of a single layer of cells with markedly cutinized outer tangential walls surrounded the culms. This epidermis was covered by a thick cuticle and contained stomata in the furrows within the epidermis, at regular intervals around the edge of the sections, and particularly at the ridges, was a hypodermis of pulviniform ribs of sclerenchyma. The ground tissue was differentiated into an outer assimilatory layer and an inner colourless parenchymatous zone.

From 20 to 100 small vascular bundles were

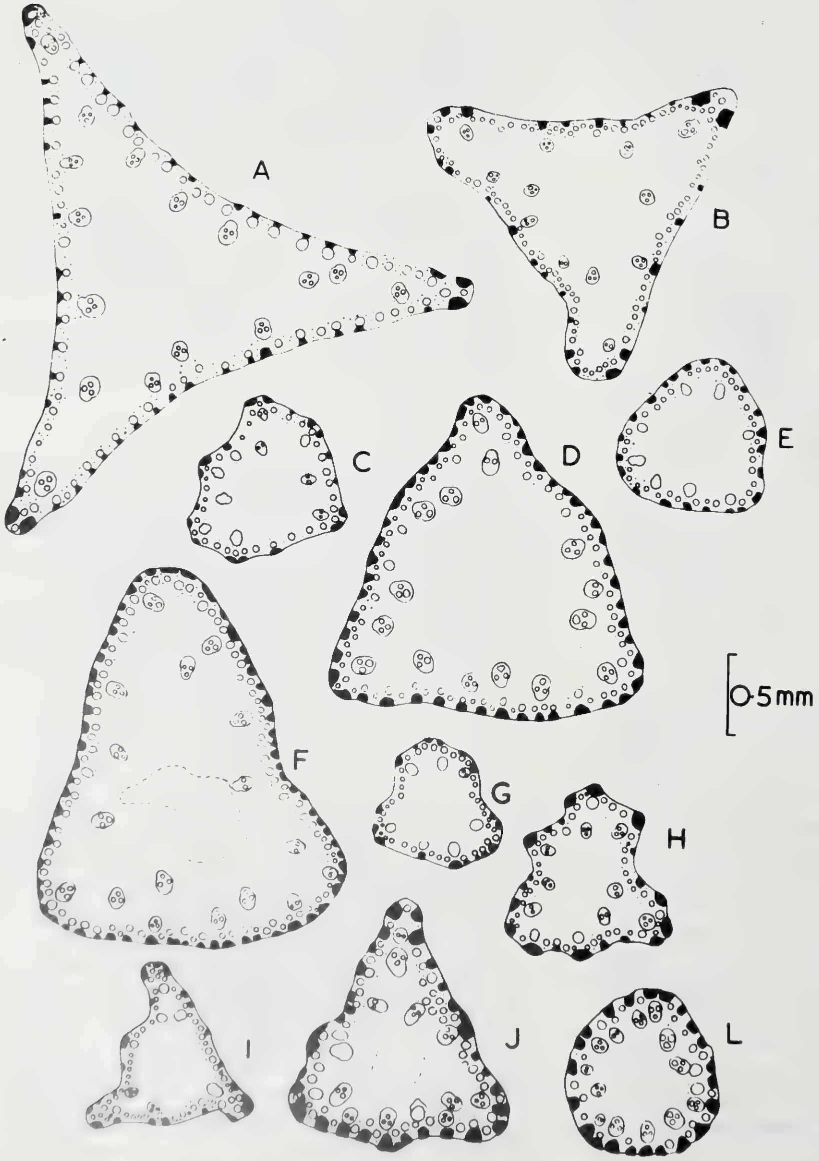

FIG. 9.—Plans of transverse sections of culms of *Kyllinga* species. A, *K. elatior* Kunth; B, *K. nemoralis* (Forst.) Dandy; C, *K. colorata* (L.) Druce; D, *K. melanosperma* Nees; E, *K. pulchella* Kunth. F, *K. polyphylla* Willd, ex Kunth., G, *K. erecta* Schum.; H, *K. odorata* Vahl; I, *K. pauciflora* Ridl.; J. *K. alba* Nees; L, *K. alata* Nees.

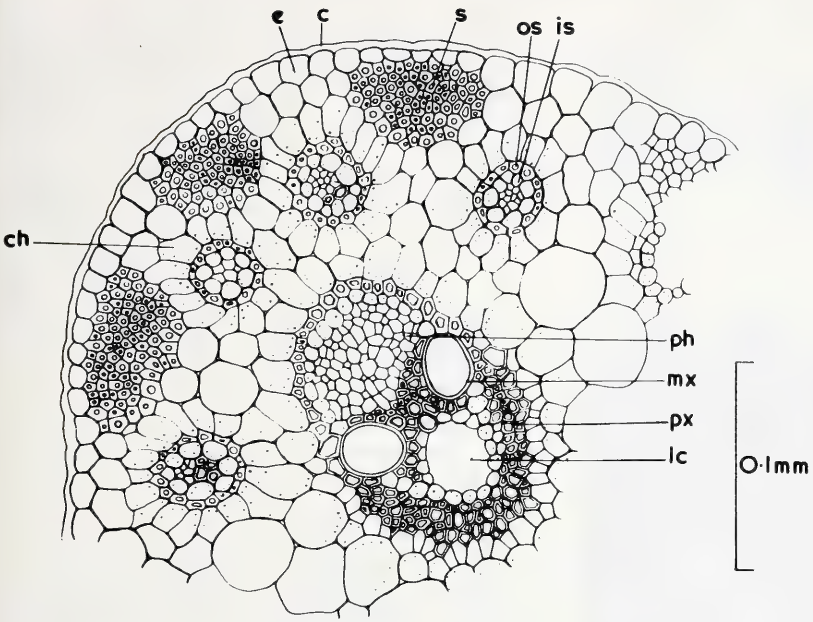

FIG. 10.—Detail of portion of transverse section of culm of *Kyllinga melanosperma* Nees. (e = epidermis; c = cuticle; s = sclerenchyma; os = outer bundle sheath; is = inner bundle sheath; chl = chlorenchymatous sheath; ph = phloem; mx = metaxylem vessel; px = protoxylem vessel; lc = lysigenous cavity.)

located in the outer regions of the ground tissue, and 12–18 larger bundles were situated nearer the centre. An extensive pith was present sometimes degenerating to form an airspace system (Fig. 9F & J).

The outer bundles, similar to the second order bundles of the leaf, had poorly defined vascular tissue surrounded by conspicuous inner chlorenchymatous and outer sclerenchymatous bundle sheaths and the characteristic radiating chlorenchyma which constituted outer assimilator-zone of the culm (Fig. 10).

Conspicuous first order bundles of the type found in the leaves were found towards the inner limits of the assimilatory zone and were associated with sclerenchyma sheaths which were better developed centripetally (Fig. 10).

Epidermal features

When describing the epidermis, Metcalfe (1960) recommended that the epidermal strip be visualized with the long axis of the leaf lying horizontally across the field. This had been done in the following description for the sake of uniformity.

The upper epidermis of the leaf consisted of horizontal parallel rows of ripple-walled cells which, in surface view, were rectangular. No stomata were seen and very little differentiation in size of epidermal cells occurred (Fig. 11).

The lower epidermis was divided into costal and intercostal regions. The cells of the intercostal zones resembled those of the upper epidermis, but were narrower. Occasionally some of the epidermal cells were shorter than neighbouring cells, but these cells were not 'short cells' of the type found in many Gramineae (Metcalfe, 1960) and they were not arranged in any definite pattern. the cells of the costal regions were long, narrow, ripple-walled cells arranged in parallel rows.

Stomata were found in horizontal bands in the intercostal regions. Narrow zones contained a single band of stomata, but up to three bands of stomata were found in wider zones. A band of stomata usually consisted of a single horizontal row of

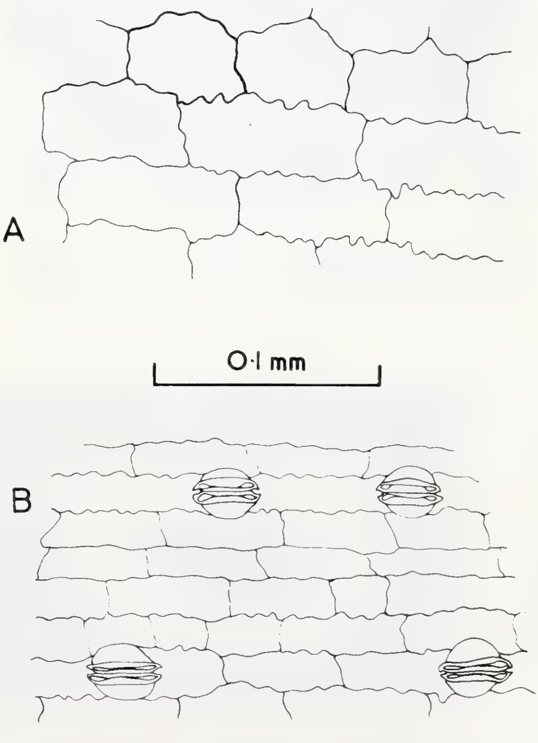

FIG. 11.—Epidermis of *Kyllinga polyphylla* Willd. ex Kunth. A, upper epidermis, B, lower epidermis intercostal zone.

alternating stomata and interstomal cells, but double rows of stomata also occurred, e.g. *K. nemoralis.*

Each stoma was bounded by two dumbbell-shaped guard cells each composed of a thickened central portion with thin-walled bulbous ends. The guard cells were flanked by subsidiary cells similar to those described by Metcalfe (1960) as 'low dome-shaped subsidiary cells' (Fig. 12).

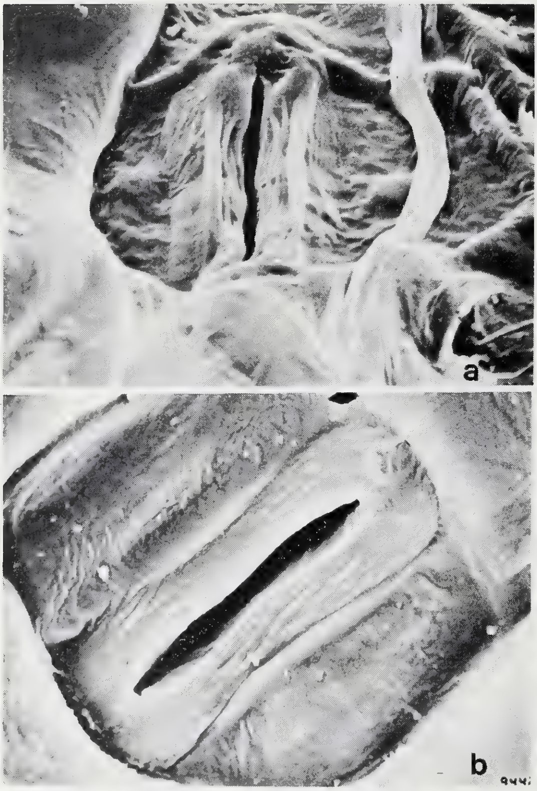

FIG. 12.—SEM of stomatal structure viewed from inner surface of epidermal strip. a, stoma of *Kyllinga colorata* (L.) Druce; b, stoma of *K. odorata* Vahl. Both approximately × 10 200.

Silica bodies were found only in epidermal cells associated with hypodermal strands of sclerenchyma. A single row of 3–8 conical silica bodies was found in each of these epidermal cells. The basic structure of the silica body is common amongst sedges.

Silica bodies when viewed at higher magnification appeared as low-domed platelets with a granular texture, the central dome surrounded by smaller satellites. The rim, unlike that of bodies described for *Rhynchospora* (Gordon-Gray *et al,* 1978) appears to be rough and irregular and not upturned (Fig. 13). Preparations also revealed the presence of silica 'skeletons' of epidermal cells suggesting that much of the epidermis was impregnated with silica.

Epidermal hairs occurred at the margins and below the keels of leaves and bracts and, in *K elatior* (*Getliffe* 12, 196, 201) hairs were also found in the intercostal regions of the leaf. Many culms of *K. alata* were also pubescent. In all species where hairs were found, the hairs were unicellular, bulbous-based and covered by a thick cuticle. The acuminate tip was orientated towards the apex of leaf or bract. The hairs of *K. alata* were visible to the naked eye and may be termed macrohairs but all others are probably better described as 'prickle-hairs' (Metcalfe, 1960). No multicellular hairs were seen (Fig. 14).

CONCLUSION

The genus shows considerable uniformity in its anatomical features which limits the use of these as taxonomic characteristics at the species level. The close relationship between *Kyllinga* and *Pycreus* detected by Turrill (1922) and their unique midrib anatomy is interesting and worth further study.

ACKNOWLEDGEMENTS

Sincere thanks are due to the Botany Department of the University of Natal, for provision of facilities for this study, to Professor K. D. Gordon-Gray for her encouragement and enthusiasm and to Mrs R. Gilliland and her staff for their help and advice.

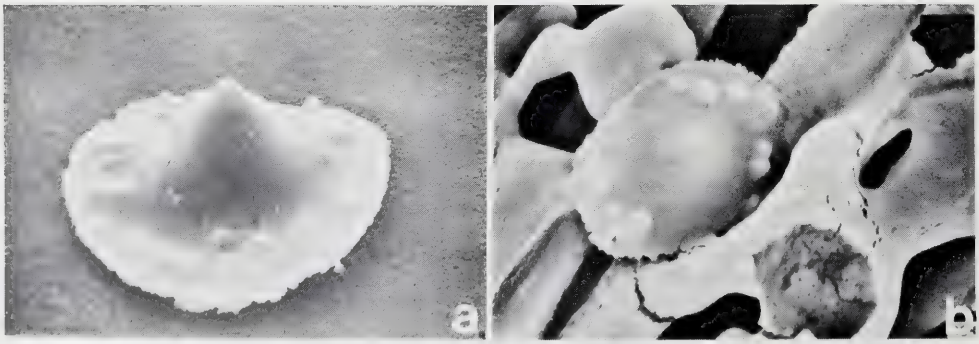

FIG. 13.—Silica remnants after digestion of leaves of *Kyllinga elatior* Kunth. showing low-domed silica body. a, silica body with conical centre and peripheral satellites. x × 13 500; b, silica body and silica outlines of epidermal cells, × 12 500.

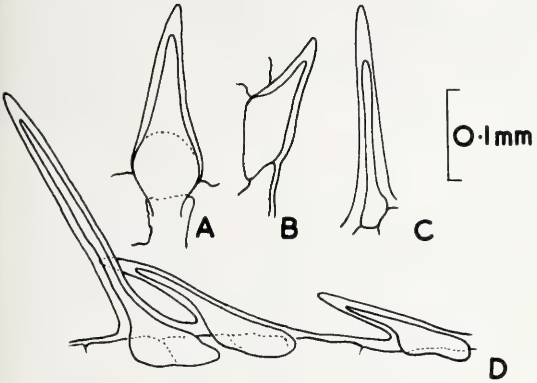

FIG. 14.—Epidermal hairs of *Kyllinga*. A + B, *K. elatior* Kunth; C + D, *K. alata* Nees.

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APPENDIX: CITATION OF SPECIMENS

K. alata *Nees*

2930 (Pietermaritzburg): The Dargle (–AC), *Getliffe 190* (NU); New Hanover, Fawn Leas (–BC), *Getliffe 169* (NU); Isipingo (–DD), *Ward 554* (NU). 2931 (Stanger): Wentworth District, Bluff (–CC), *Ward 4980* (NU); do. *Getliffe 1008* (J). 3029 (Kokstad): Bedford Farm Harding District (–DB), *Lennox s.n.* (NU).

K. alba *Nees*

2628 (Johannesburg): Benoni Golf Course (–AB), *Villet 3010* (J). 2632 (Bela Vista): Ndumu Game Reserve (–CD), *Ross 693* (NU). 2732 (Ubombo): Ubombo Village (–CA), *Getliffe 162* (NU).

K. colorata *(L) Druce*

2930 (Pietermaritzburg): Chase Valley (–CB), *Getliffe 23* (NU); University of Natal (–CB), *Getliffe 191* (NU); Botanic Gardens (–CB), *Ross 993* (NU); King Edward Avenue (–CB), *Getliffe 998, 999* (J).

K. elatior *Kunth.*

2830 (Dundee): Kranskop, Middledrift Road (–DD), *Getliffe 12* (NU). 2930 (Pietermaritzburg): Town Bush Valley, Cascade Falls (–CB), *Getliffe 196* (NU); Pinetown, B (–DD) *Getliffe 1005* (J); 2931 (Stanger): Inanda District, Mt. Edgecombe *Getliffe 201* (NU).

K. erecta *Schum.*

2930 (Pietermaritzburg): Thomas Moore School (–DD), *Getliffe 176* (NU); Pinetown (–DD), *Getliffe 1006.* (J).

K. melanosperma *Nees*

2429 (Zebediela): near Potgietersrus (–AA), *Edwards s.n.* (J).

K. nemoralis *(Forst.) Dandy*

2931 (Stanger): Durban Country Club Golf Course (–CC), *Getliffe 193* (NU); Durban Botanic Gardens (–CC), *Getliffe 996* (J).

K odorata *Vahl.*

2930 (Pietermaritzburg): Thomas Moore School, Pinetown, (–DD), *Getliffe 175;* do. *Getliffe 1004* (J).

K. pauciflora *Ridl.*

2930 (Pietermaritzburg): Lions River District, Rawdons Hotel (–AC), *Getliffe 224* (NU); Hermansburg District, vlei near school (–BB), *Getliffe 174* (NU); Impendhle Tillietudlem (–DB), *Getliffe 265* (NU).

K. polyphylla *Willd. ex Kunth*

2931 (Stanger): Durban, Windsor Park Golf Course (–CC), *Getliffe 28, 164, 292* (NU), do. *Getliffe 1010* (J).

K. pulchella *Kunth*

2930 (Pietermaritzburg): Lion's River District, Karkloof (–AC), *Getliffe 205B* (NU). 2629 (Bethal): 27 k from Standerton (–CC), *Getliffe 1011* (J).

Bothalia 14, 3 & 4: 819–823 (1983)

The genus *Schoenoxiphium* (Cyperaceae). A preliminary account

I. KUKKONEN*

ABSTRACT

The genus *Schoenoxiphium* of the tribe Cariceae of Cyperaceae is conservatively accepted as being restricted to the African continent and Madagascar. The special features of the inflorescence structure are described. The following species are provisionally recognized: *S. basutorum* Turrill, *S. distinctum* Kukkonen, *S. ecklonii* Nees, *S. filiforme* Kükenthal, *S. gracile* Chermezon, *S. lanceum* (Thunberg) Kükenthal, *S. lehmannii* (Nees) Steudel, *S. madagascariense* Chermezon, *S. perdensum* Kukkonen, *S. rufum* Nees, *S. schweickerdtii* Merxmüller & Podlech, and *S. sparteum* (Wahlenberg) Kükenthal. A key to the species is provided and their distribution is roughly outlined. The morphological variation within the species suggests separation of taxa below specific level, or perhaps even at species level, but this will require more detailed information about the ecology, distribution and the cytology.

RÉSUMÉ

LE GENRE SCHOENOXIPHIUM *(CYPERACÉES). NOTE PRÉLIMINAIRE*

Le genre Schoenoxiphium *de la tribu des Caricées dans les Cypéracées est classiquement accepte comme étant restreint au continent africain et à Madagascar. Les caractères spéciaux de la structure de l'inflorescence sont décrits. Les espèces suivantes sont provisoirement reconnues:* S. basutorum *Turrill,* S. distinctum *Kukkonen,* S. ecklonii *Nees,* S. filiforme *Kükenthal,,* S. gracile *Chermezon,* S. lanceum *(Thunberg) Kükenthal,* S. lehmannii *(Nees) Steudel,* S. madagascariense *Chermezon,* S. perdensum *Kukkonen,* S. rufum *Nees,* S. schweickerdtii *Merxmüller & Podlech et* S. sparteum *(Wahlenberg) Kükenthal. Une clef de ces espèces est présentée et leur aire de répartition est indiquée dans ses grandes lignes. La variation morphologique à l'intérieure de l'espèce suggère une séparation des taxons au niveau infra-spécifique ou peut être même au niveau spécifique, mais ceci nécessitera plus d'informations détaillées sur l'écologie, la répartition et la cytologie.*

The generic limits within the tribe Cariceae of Cyperaceae are obscure. It seems clear, however, that the whole tribe comprises a well-defined and coherent group. Kükenthal (1909) in his monograph understood it to represent a sub-family and distinguished four genera: *Schoenoxiphium, Kobresia, Uncinia* and *Carex.*

It seems to be accepted that the different inflorescence structures exhibit stages in a process of inflorescence reduction, early outlined by Pax (1886, also in Kükenthal, 1909) and discussed by several later authors. A detailed description of this process based on anatomical evidence, however, is still to be given.

It is generally agreed that the reduction proceeded from a large paniculate inflorescence towards, ultimately, a spike. Simultaneously with the reduction in size, specialization took place within the inflorescence. The unisexual flowers became grouped together in different parts of the inflorescence, finally forming separate unisexual spikes (e. g. as in *Carex*).

Kükenthal (1909) suggested that the genera represent, roughly, successive stages in the general reduction, the genus *Schoenoxiphium* having the least advanced inflorescences, and *Uncinia* and *Carex* with their closed utricles the most advanced types. This might have been plausible at the beginning of the century, but since then much more material has been accumulated and it is now evident that the genera cannot be arranged in a simple linear sequence. It is also evident that the genera *Kobresia* and *Schoenoxiphium* are badly in need of a taxonomic revision.

Ivanova (1940) produced a revision of the genus *Kobresia* and made a number of new combinations. For example, she transferred several *Carex* species to *Kobresia* and some *Kobresia* species with panicled inflorescences to *Schoenoxiphium.* The bulk of the present *Schoenoxiphium* species she assigned to a new genus, to which she applied the name *Archaeocarex.* Her suggestions, although they have never been definitely rejected, have not been followed.

The inflorescence of both *Kobresia* and *Schoenoxiphium* are rather variable in structure and size. They both show relationships to certain species of *Carex.* To merge *Schoenoxiphium* with *Kobresia* does not, of course, produce any additional evidence of the relationship of these genera (Koyama, 1961). — Kükenthal (1909) gave the restriction of *Schoenoxiphium* to Africa, and the absence of *Kobresia* there, as one reason for keeping these genera separate. Later, however, he described *Schoenoxiphium kobresioideum* from Sumatra (Kükenthal, 1940). This species was subsequently transferred to *Kobresia* by Kern (1958).

Therefore, the genus *Schoenoxiphium* as understood in this paper, occurs only on the African continent and Madagascar (Kukkonen, 1978). The

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aim of this study is to give a preliminary overview of the genus in this context.

On the inflorescence structure of Schoenoxiphium

An essential prerequisite for defining the genus *Schoenoxiphium* and its species is a clear idea of the inflorescence structure. In addition, for accurate identification of the species, mature utricles are required.

The inflorescence vary from a large panicle to, occasionally, a single spike. Mostly, they are branched structures, and it may be noted that a utricle is formed only when the inflorescence branches. The utricle is a prophyll, i.e., the first leaf, or rather the modified sheath of the first leaf on the branch. In the lower parts of the inflorescence, at the base of the large first order branches, it may be sterile. If, in addition, it narrowly sheaths the branch, it can be called a cladoprophyll (Kükenthal, 1909). The branch thus grows through the utricle.

A fertile utricle encloses a single pistillate flower. There are no other pistillate flowers on the same branch. Only staminate flowers with their glumes occur on the branch above the pistillate flower. The branch may, however, rebranch and at the base of the new branches utricles again occur, but these are then each on a branch of the next higher order.

Towards the periphery of the inflorescence the branches protruding from the utricles are smaller, bearing only a few staminate flowers, or remaining sterile. Basically, the word 'rachilla' is used here to denote such a sterile, rudimentary branch, either protruding from the utricle or remaining completely enclosed in it, but this term is sometimes modified with the words fertile or sterile (Figs 1 & 2).

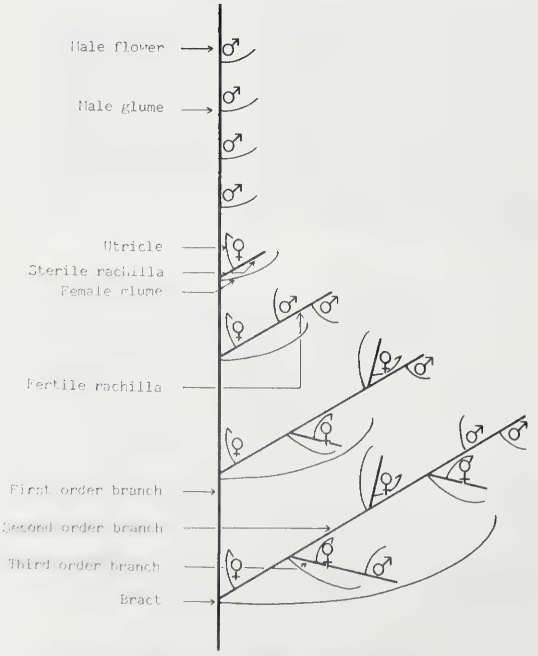

FIG. 1.—Structure of a lower first order branch of a *Schoenoxiphium* inflorescence.

Each branch is produced in the axil of its bract. The bracts of the lowest branches are usually large and leaf-like. A male glume supports the staminate flower. The female glume is homologous with the bracts but as applied here the term refers to a bract supporting the utricle with the female flower and with, as a rule, only a sterile rachilla branch.

The utricle is rather variable, even within the same inflorescence; at the base of the first-order branch, if this is fertile, it is frequently split wide open. In this case a beak can hardly be distinguished. At the base of the ultimate branches, which frequently remain sterile, the utricles are almost closed and flask-shaped, and, when present, the beak is well defined.

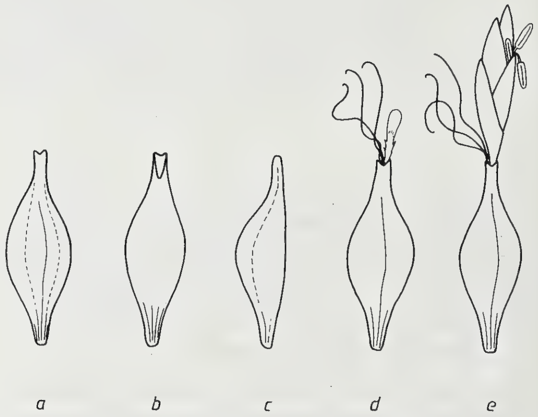

FIG. 2.—Utricle of a *Schoenoxiphium* species: a, from abaxial side; b, from adaxial side with oblique ostiole; c, side view of a plenoconvex utricle; d, utricle with protruding sterile rachilla and three stigmas; e, utricle with fertile rachilla.

Some of the morphological characters are summarized in Table I. The data were mainly obtained from the type specimens, which were studied whenever possible. The inflorescence measurements relate to a single apical inflorescence or to a compact terminal group of lateral inflorescences. Unless otherwise mentioned, the measurements of both the utricles and glumes relate to structures on the ultimate branches of the inflorescence. The length of a utricle includes the beak and, when present, the stipe.

TABLE 1. – ***Schoenoxiphium*** species: summary of some of the morphological characters

	Height	Stem diam.	Length of basal sheaths	Length of ligule	Width of leaf blades	Size of inflorescence	Length of vagina of lowest bract	Branching of inflor-escence (highest order)	Female glumes	Utricles	Beak	Fruit
	cm	mm	mm	mm	mm	mm	mm		mm	mm	mm	mm
S. rufum	40–60	1,5–2,0	40	0,2	4,0–5,5	35×15	30	2nd	3,0–4,0×1,6	4,2×1,6	0,7	2,5×1,5
S. schweickerdtii	70–95	2,5–3,5	40–80	0,7	7,5–11,0	40–60×20–35	50	3rd	7,0–8,4×1,8–2,0	7,0–9,0×0,7–2,0	2,2–3,0	4,2–5,2×0,6–1,6
S. lanceum	70–120	1,4–2,6	50–80	0,2	6,0–8,5	120×20	60	3rd	6,0–8,0×0,7–1,1	5,4–6,6×0,7–1,1	0,9–1,5	4,0×0,8
S. perdensum	25–30	c.0,5	25	0,2	0,5–1,0	10	28	4th	4,0	3,4–3,5×0,6–0,9	0,6–0,9	2,7×1,6
S. filiforme	30	c.0,5	20–30	0,4	c.0,5	10–15	25	1st	3,3–4,3×1,2–1,4	3,5–3,8×0,8–1,0	1,0–1,2	2,5×0,9
S. sparteum	30–70	c.1,0	25–45	0,2	2,0–4,0	15–20×12–15	35	2nd	3,0–4,5×1,0–1,7	2,3–2,9×1,3–1,7	0,1–0,6	1,9–2,3×c.1,4
S. lehmannii	30–70	1,0–1,5	15–45	0,3	2,5–4,0	7–25×5–7	35	3rd	3,5–6,7×0,9–1,8	4,7–5,5×1,5–1,7	1,3–1,8	2,5–3,2×1,4–1,5
S. madagascariense	50–85	1,5–2,0	50–80	0,3	6,0–8,0	70–80×45–65	0	4th	3,4–10,3×0,8–1,7	7,0–9,3×0,7–1,8	2,0	3,5–4,5×0,7–0,8
S. gracile	40–80	c.1,0	25–30	0,2	1,5–3,5	60×10	0	4th	4,2	4,9–7,2×0,6–0,9	2,0–2,2	2,5–3,3×0,7–0,9
S. ecklonii	15–30	c.1,0	20–25	c.0,2	2,0–3,0	25×10	0	2nd	5,5×2,3	5,2–5,5×1,1–1,5	±0	4,5×1,4
S. basutorum	30–40	0,5–1,0	20–30	0,3–0,5	1,0–1,5	25–40×7–15	0	2nd	5,7–6,3×0,8–1,0	6,5–7,0×0,8–1,0	1,6–1,8	4,5×0,7
S. distinctum	12–17	c.0,8	20	0,25	1,5–2,5	25–30	0	2nd	3,5–4,0×0,7–0,8	3,5–4,0×0,7–0,8	0,8	2,5–2,8×c.0,6

KEY TO THE SPECIES

1. Bracts with a vagina 25–60 mm long 2
   Bracts evaginate 8

2. Robust plants, 40–120 cm tall; leaves 4,0–8,5 mm wide; stem 1,5–3,5 mm thick 3
   Small or slender plants, 25–70 cm tall; leaves 0,5–4,0 mm wide; stem 0,5–1,5 mm thick 5

3. Plants 40–60 cm; utricles 4,0–4,5 mm; glymes 3,0–4,0 mm long .... *S. rufum*
   Plants 70–120 cm; utricles 5,4–9,0 mm; glumes 6,0–8,4 mm long 4

4. Plants 70–95 cm; stem 2,5–3,5 mm; leaves 7,5–11,0 mm wide; utricles 7,0–9,0 mm long .... *S. schweickerdtii*
   Plants 70–120 cm; stem 1,4–2,5 mm; leaves 6,0–8,5 mm wide; utricles 5,4–6,6 mm long .... *S. lanceum*

5. Plants 25–30 cm; stem c. 0,5 mm; leaves 0,5–1,0 mm wide 6
   Plants 30–70 cm; stem 1,0–1,5 mm; leaves 2,0–4,0 mm wide 7

6. Inflorescence composed of up to 5–6 partial inflorescences along the stem; utricles planoconvex, without suberous base and never finally reflexed .... *S. perdensum*
   Inflorescence one terminal spike or with one (or a few) lateral, partial inflorescence; utricles cylindrical; base suberous, finally reflexed .... *S. filiforme*

7. Plants rigid, inflorescence a rather compact and rigid panicle; utricles 2,0–3,0 mm, with a beak less than 1,0 mm long .... *S. sparteum*
   Plants slender; inflorescence lax, slender; utricles stipitate, 4,7–5,5 mm, with a beak 1,3–1,8 mm long .... *S. lehmannii*

8. Plants 40–85 cm; inflorescences large, 60–80 mm long, 4th order branches present 9
   Plants 12–40 cm; inflorescences small, 7–40 mm long, branches up to 2nd order 10

9. Inflorescence large, rounded, 70–80 × 45–65 mm; utricles 7,0–9,3 mm long .... *S. madagascariense*
   Inflorescence small, narrow, c. 60 × 10 mm; utricles 4,9–7,2 mm long .... *S. gracile*

10 Plants 15–40 cm; glumes 5,5–6,3 mm; utricles 5,2–7,0 mm; fruit c. 4,5 mm long 11
   Plants less than 20 cm tall; glumes 3,0–4,0 mm; utricles 3,5–4,0 mm and fruits 2,5–2,8 mm long .... *S. distinctum*

11. Leaves 2,0–3,0 mm wide; utricles 5,2–5,5 mm, beakless .... *S. ecklonii*
    Leaves 1,0–1,5 mm wide; utricles 6,5–7,0 mm, with a beak 1,6–1,8 mm long .... *S. basutorum*

SYNOPSIS OF THE SPECIES

Schoenoxiphium rufum *Nees* in Linnaea 10: 201 (1836). Lectotype (selected here): 'Ceded Territory, bei Phillipstown am Katrivier', 2 000–3 000′, leg. *Ecklon & Zeyher* (S!). Fig. 3.

S. buchananii C. B. Cl. in Dur. & Schinz, Consp. Fl. Afr. 5: 676 (1895).
S. ludwigii Hochst. in Krauss, Flora, Jena 48: 764 (1845).

Schoenoxiphium schweickerdtii *Merxm. & Podlech* in Mitt. bot. St. Samml. Münch. 4: 529 (1960). Holotype: Transvaal, Drakensberge, Mariepskop, 2 000 m, *Merxmüller* 590 (M!). Fig. 4.

Schoenoxiphium lanceum *(Thunb). Kükenth.* in Pflanzenreich IV. 20 (38): 28 (1909). Type: In herb. *Thunberg,* (UPS!). Fig. 4.

Schoenus lanceus Thunb., Prodr. p. 17, (1794).
S. sickmannianum Kunth, Enum. Pl. 2: 530 (1837).
S. meyerianum Kunth, Enum. Pl. 2: 530 (1837).
Carex ramosa Eckl. ex Nees in Linnaea 7: 533 (1833), non Schkuhr.

Schoenoxiphium perdensum *Kukkonen* in Bot. Notiser 131: 265 (1978). Holotype: Cape Prov., Distr. King William's Town, Keiskama Hoek, near Ghulu Kop, 4 000′, 1925, *R. A. Dyer* 245a (K!; K, iso.!). Fig. 4.

Schoenoxiphium filiforme *Kükenth.* in Kew Bull. Misc. Inf., p. 129 (1910). Holotype: S. Africa, Cape Prov., 'Summit of Great Winterberg', 7 700′, March 1900, *Galpin* 5605 (K!). Fig. 4.

Schoenoxiphium sparteum *(Wahlenb.) C. B. Cl.* in Kew Bull. Misc. Information, Add. series 8: 67 (1908). Type: in Herb. *Thunberg* (UPS!). Fig. 3.

Carex spartea Wahlenb. in K. Svenska Vetensk. Akad. Handl. 24: 149 (1803).

S. schimperianum (Boeck.) C. B. Cl. in Kew Bull. Add. Ser. 8: 67 (1908).

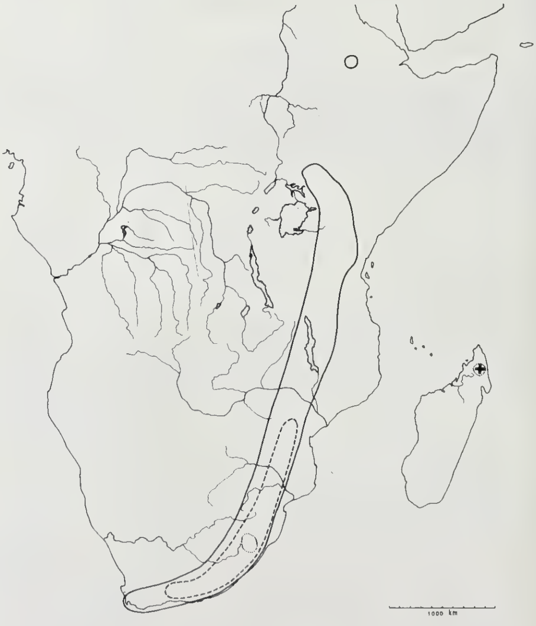

FIG. 3.—Distribution of five *Schoenoxiphium* species: — *S. lehmannii* and *S. sparteum* (northernmost area in Ethiopia is *S. sparteum*); — — *S. rufum;* ...... S. madagascariense; + *S. gracile.*

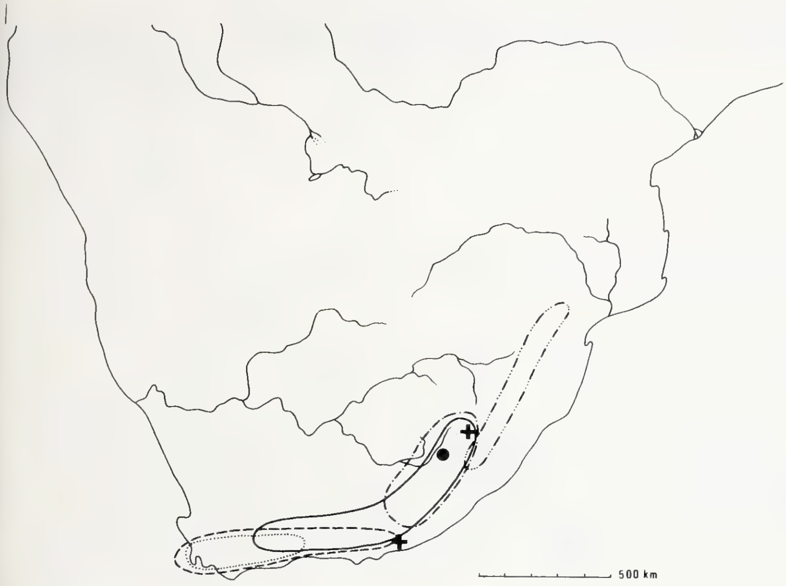

FIG. 4.—Distribution of seven *Schoenoxiphium* species: — *S. basutorum;* — —*S. ecklonii;* ...... *S. lanceum;* —.— *S. filiforme;* —...— *S. schweickerdtii;* + *S. perdensum;* ● *S. distinctum.*

Carex schimperiana Boeck. in Linnaea 40: 373 (1876).
S. kunthianum Kükenth. in Pflanzenreich IV. 20 (38): 31 (1909).
Carex bolusii C. B. Cl. in T.-Dyer, Fl. Cap. 7: 304 (1898).
S. caricoides C. B. Cl. in Kew Bull. Add. Ser. 8: 67 (1908).

Schoenoxiphium lehmannii *(Nees) Steudel,* Synopsis Pl. Glumac. 2: 245 (1855). Lectotype (selected here): 'Cap, östlicher Abhang des Tafelberges, bei Konstantia', *Ecklon & Zeyher* (S!). Fig. 3.

Uncinia lehmannii Nees in Linnaea 10: 206 (1836).
Carex uhligii K. Schumann ex C. B. Cl. in Kew Bull. Add. Ser. 8: 73 (1908).

Schoenoxiphium madagascariense *Cherm.* in Bull. Soc. bot. Fr. 70: 299 (1923). Holotype: 'Madagascar Centre, Mont Tsaratanana', 2 700 m, déc. 1912. *Perrier de la Bathie* 2501 (P!). Fig. 3.

Schoenoxiphium gracile *Cherm.* in Bull. Soc. bot. Fr. 70: 300 (1923). Holotype: Mont Tsaratanana, *Perrier de la Bathie* 2502 (P!). Fig. 3.

Schoenoxiphium ecklonii *Nees* in Linnaea 10: 200 (1836). Lectotype (selected here): 'Adowhügel, 3' et., 'Distr. Uitenhagen,' Oct. 1829, *Ecklon & Zeyher* 909 (SAM!; S, isolecto.!). Fig. 4.

Schoenoxiphium basutorum *Turrill* in Kew Bull. Misc. Inf., p. 14 (1914). Holotype: Lesotho, Leribe, Dec. 1913, *Dieterlen* 948 (K!). Fig. 4.

Schoenoxiphium distinctum *Kukkonen* in Bot. Notiser 131: 263 (1978). Holotype: Lesotho, between Indumeni Dome and Castle Buttress, locally common in alpine grassveld on summit of Drakensberg, 9 800', 10.12.1957, *Killick* 2274 (BM!; K, iso.!). Fig. 4.

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Morphologie et palynologie des Annonacées africaines: interrelations phylogéniques

A. LE THOMAS*

RÉSUMÉ

La taxonomie n'est pas seulement un système de classification pratique, mais aussi une science de synthèse qui tente de schématiser les étapes possibles suivies par l'évolution d'un groupe. Elle cherche donc à recréer et expliquer la dynamique de l'évolution des végétaux à partir de l'analyse de l'ensemble de leurs caractères et des relations qui existent entre eux.

Ainsi, elle ne peut que bénéficier de la naissance ou du développement de toutes les disciplines qui analysent de nouveaux composants végétaux ou les étudient dans le temps ou dans l'espace. A ce double titre, la Palynologie a pris un essor considérable en taxonomie, apportant de nouveaux caractéres morphologiques dont la comparaison peut se faire avec de nombreux témoins fossiles.

Dans la famille des Annonacées, dont chacun s'accorde à reconnaitre l'aspect artificiel des différentes classifications, l'étude du pollen a permis de montrer que l'évolution s'exprime en séries morphologiques continues dans des lignées parallèles. Les corrélations établies avec d'autres caractères morphologiques mettent alors en lumière certains phénomènes d'évolution parallèle dans la famille qui tendent à montrer que la fleur des Annonacées est une structure en voie de réduction, et contribuent à une meilleure connaissance des affinités entre les taxons génériques et de leurs niveaux évolutifs respectifs.

ABSTRACT

MORPHOLOGY AND PALYNOLOGY OF THE AFRICAN ANNONACEAE: PHYLOGENETIC INTER-RELATIONS

Taxonomy is not only the practice of plant classification, but also a science of synthesis attempting to outline the possible stages followed by the evolution of a group. It attempts, therefore, to re-create and to explain the dynamics of the evolution of plants through the analysis of all their characters and of the relationships existing between them.

Consequently, it can only benefit from the birth or development of all disciplines that analyse fresh aspects of plants or study them in time and space. For these reasons, palynology has developed considerably within taxonomy, revealing new morphological characters that permit a comparison with many fossil examples.

In the family Annonaceae, of which the different classifications are admittedly artificial, pollen studies have shown that evolution is expressed in continuous morphological series along parallel lines. The established correlations with other morphological characters throw some light on certain phenomena of parallel evolution within the family, showing that the flower of the Annonaceae is in the process of reduction and the correlations contribute to a better knowledge of the affinities between generic taxa and their respective evolutionary levels.

INTRODUCTION

La taxonomie végétale est une science de synthèse qui tente de schématiser les étapes de l'évolution des plantes. Elle cherche donc à recréer et expliquer la dynamique de l'évolution des végétaux à partir de l'analyse de l'ensemble de leurs caractères et des relations qui existent entre eux. Ainsi, elle ne peut que bénéficier de la naissance ou du développement de toutes les disciplines qui analysent de nouveaux composants végétaux ou les étudient dans le temps ou dans l'espace. A ce double titre, la Palynologie a pris un essor considérable en taxonomie apportant de nouveaux caractères morphologiques dont la comparaison peut se faire avec de nombreux témoins fossiles.

L'étude du pollen aide donc à répondre aux questions fondamentales du taxonomiste: l'origine des formes, leurs affinités et leurs rapports phylogéniques. C'est ainsi que, chez les Annonacées, les caractères polliniques permettent de mieux illustrer les interrelations phylogéniques des autres caractères morphologiques de la famille.

LES FAITS PALYNOLOGIQUES

La morphologie pollinique des Annonacées africaines (Fig. 1) permet de dégager trois grands types de pollens (Le Thomas, 1981):

un type simple, sulqué distal, très hétéropolaire,
un type simple inaperturé,
un type en tétrade acalymée, subcarrée plane, rhomboïdale ou tétrahédrique; des polyades existent également dans le genre *Xylopia*.

L'étude de l'ultrastructure des parois polliniques a conduit à mettre en évidence une dissymétrie comparable dans la répartition de l'exine des pollens simples sulqués *(Ambavia)*, inaperturés *(Isolona)* ou en tétrades *(Asteranthe)*, ce qui permet de montrer que la modification de l'exine à la face proximale des pollens en tétrades ne peut être morphologiquement interprétée comme une aperture. Les pollens composés sont donc de type inaperturé, ce qui entraîne déjà vers une première conclusion dans l'évolution du pollen des Annonacées. En effet, le type sulqué hétéropolaire étant actuellement considéré par l'ensemble des palynologues comme le plus primitif des Angiospermes (Walker & Doyle,

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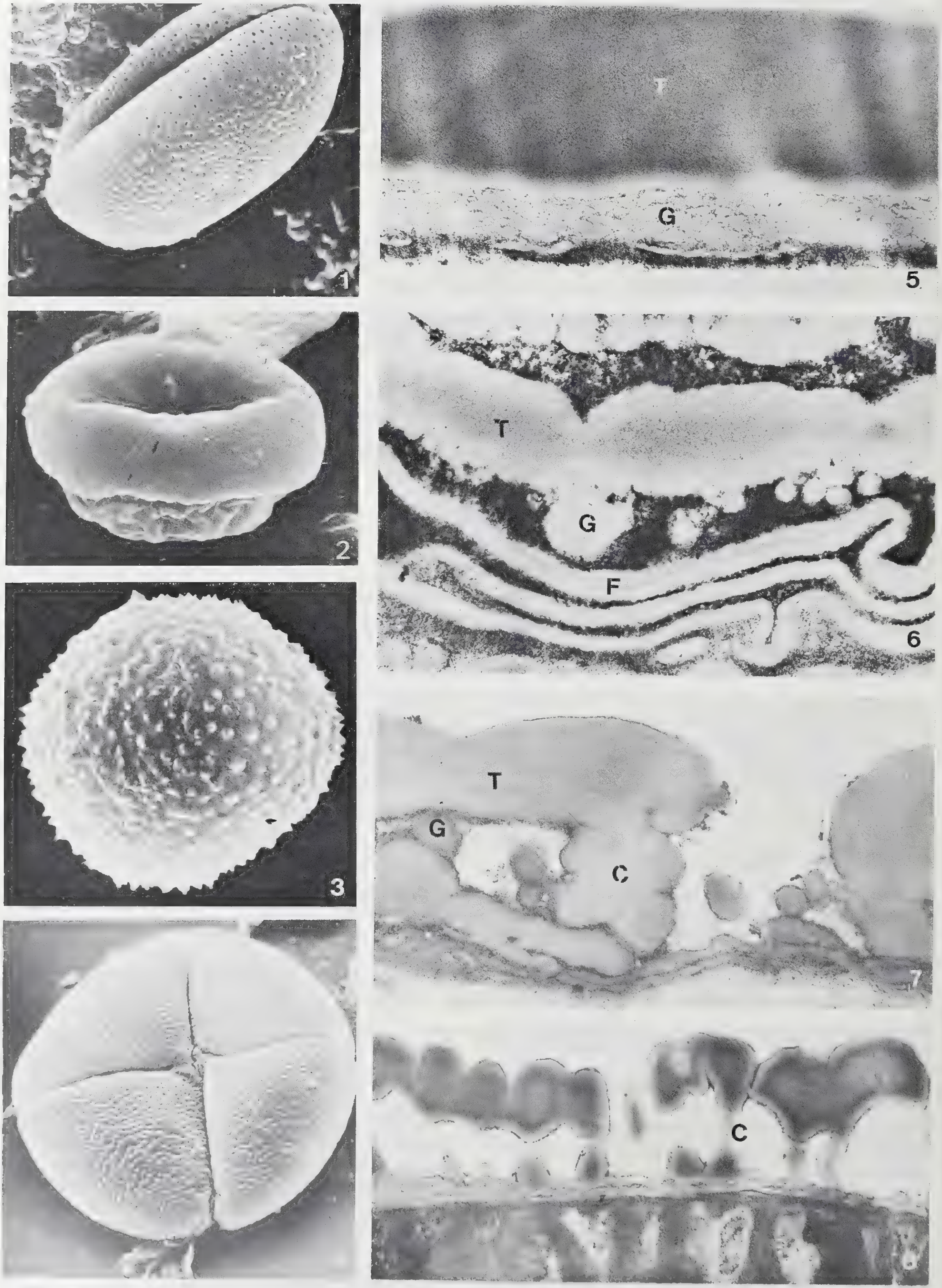

FIG. 1.—Types morphologiques du pollen des Annonaceae. 1, hétéropolaire sulqué distal, *Polyalthia capuronii*, × 1 500 (MEB); 2, conique, sulqué distal, *Ambavia gerrardii*, × 2 300; 3, sphérique inaperturé × 3 700; tétrade inaperturée subcarrée plane, *Uvariastrum pierreanum*, × 900; 4, types de structures exiniques; 5, structure infratectale grenue peu différenciée sans couche basale (foot-layer), *Lettowianthus stellatus*, × 35 000; 6, structure grenue à couche basale feuilletée lamellaire, *Uvaria klaineana*, × 50 000; 7, structure mixte, columelles constituées par la soudure de gros grains et grains isolés, couche basale feuilletée lamellaire, *Mischogyne elliotianum*, × 40 000; 8, structure columellaire à couche basale feuilletée, *Artabotrys thomsonii*, × 15 000. (MET, B. Lugardon, Lab. Biol. Végétale, Toulouse.)

1975), il n'a pu évolué dans cette famille que vers une perte générale de l'aperture.

Si d'autre part, on examine la structure de l'exine, on peut également y reconnaître trois grands types (Le Thomas, 1981):

des exines à structure infratectale grenue (Van Campo *et al.*, 1973),
des exines à structure infratectale columellaire,
des exines à structure infratectale intermédiaire ou mixte.

Etant associés à des types d'ornementation très variés et représentés dans les différents types morphologiques polliniques, aucun de ces types d'exine ne peut être retenu comme caractère taxonomique.

Dans le genre *Polyalthia*, par exemple, le type pollinique sulqué est conservé alors que la structure de l'exine montre un échantillonnage presque complet de celle que l'on observe dans l'ensemble de la famille. Séparer la structure grenue de la structure columellaire aurait pu tenter certains palynologues non systématiciens, et cela aurait conduit à scinder le genre *Polyalthia* (Fig. 2) de façon tout-à-fait artificielle, alors qu'il est par ailleurs très homogéne. Au contraire, cette série structurale continue permet de montrer que le grain, même à l'état peu différencié, est l'homologue de la columelle.

Mais, pour comprendre l'enchaînement de ces structures exiniques, et pouvoir leur donner une signification taxonomique, il est nécessaire de déterminer le sens évolutif de cette série. C'est alors qu'interviennement les interrelations morphologiques et palynologiques.

S'il est difficile de s'appuyer sur les grandes coupures taxonomiques de la famille, en raison de leur caractère souvent très artificiel (Fries, 1958; Le Thomas, 1969), on ne peut cependant manquer d'observer dans certains caractères morphologiques une tendance évolutive très nette dont la comparaison avec le pollen devient particulièrement intéressante.

CORRÉLATIONS MORPHOLOGIQUES ET PALYNOLOGIQUES

1. L'étape évolutive la plus spectaculaire chez les Annonacées est, sans conteste, le passage d'un gynécée apocarpe à un ovaire uniloculaire à placentation pariétale, se développant en un véritable syncarpe uniloculaire. Ce cas n'existe que dans les deux genres africains: *Isolona et Monodora,* chez lesquels le pollen est toujours inaperturé, simple ou en tétrade. La structure de l'exine est de type mixte ou intermédiaire, avec toujours une couche basale feuilletée lamellaire, parfois même organisée, c'est-à-dire massive dans sa partie supérieure. Elle n'est jamais de type grenu peu différencié et dépourvu de couche basale, comme chez *Polyalthia stuhlmannii* par exemple. Dans le cas de ces deux genres, particulièrement évolués sur le plan de la morphologie florale, il semble donc que l'évolution du pollen s'accompagnerait de la perte de l'aperture et de l'acquisition d'une structure exinique intermédiaire ou mixte avec trois couches.

2. Une autre tendance évolutive très nette s'observe également dans la réduction des cycles de la corolle. A partir du type classique à deux cycles alternes de trois pétales égaux (*Uvaria*), on remarque que trois genres seulement ne possèdent plus qu'un seul cycle. Ce sont encore trois genres africains. Les nombreux stades intermédiaires présents dans d'autres genres permettent de montrer que les *Enantia* ont perdu leur cycle externe, les *Dennettia* leur cycle interne, et les *Uvariopsis* un pétale de chaque cycle, les pétales étant soudés en un seul cycle. A ces trois genres, chez lesquels la réduction de la corolle est totalement réalisée, correspondent des pollens dont la structure exinique est soit grenue-columellaire chez *Uvariopsis,* soit vraiment columellaire chez *Enantia* et *Dennettia,* quelque soit le type pollinique, simple sulqué ou composé inaperturé. Autrement dit, on constate encore dans ce cas, qu'à un niveau floral avancé, correspond dans le pollen une structure exinique de type intermédiaire ou columellaire, mais jamais grenue. La structure columellaire apparaît donc là aussi comme une structure dérivée.

Par analogie, il devient donc possible d'orienter la série structurale du pollen de *Polyalthia* vers une acquisition de la columelle à partir d'une structure grenue peu différenciée (*P. stuhlmannii*), cette acquisition s'accompagnant d'un ensemble de modifications de l'exine dans les différentes couches, et non nécessairement liées à un changement de type pollinique.

Cette série structurale devient en quelque sorte l'indicateur évolutif fondamental de la famille puisqu'on la retrouve pratiquement à tous les niveaux, exprimée soit par une seule étape, soit par des séquences de différenciation réduites à quelques étapes. Des séries comparables ont été récemment trouvées par Doyle *et al.* (1979) dans les pollens monosulqués d'Angiospermes du Crétacé inférieur gabonais, apportant ainsi des éléments paléobotaniques susceptibles de soutenir cette interprétation phylogénique du pollen des Annonacées.

SÉRIES PHYLOGÉNIQUES DU POLLEN

L'étude morphologique et structurale du pollen des Annonacées conduit donc à définir les deux grand axes de l'évolution: 1, la perte de l'aperture avec l'acquisition d'un type inaperturé simple, puis composé; 2, la différenciation de l'exine vers une structure columellaire à partir d'une structure grenue très peu différenciée.

Il devient alors possible de cerner avec précision le type pollinique de base de la famille: hétéropolaire, sulqué, à tectum épais continu, microperforé, et structure exinique grenue très peu différenciée (Fig. 3), dépourvue de couche basale, tel que celui du genre *Piptostigma* (Le Thomas & Lugardon, 1974), et seulement connu par ailleurs chez les Dégenériacées (Walker & Skvarla, 1975).

A partir de ce type, les tendances majeures de l'évolution du pollen se manifestent suivant quatre séries parallèles qui soulignent des niveaux évolutifs différents pour des formes ou des structures identiques.

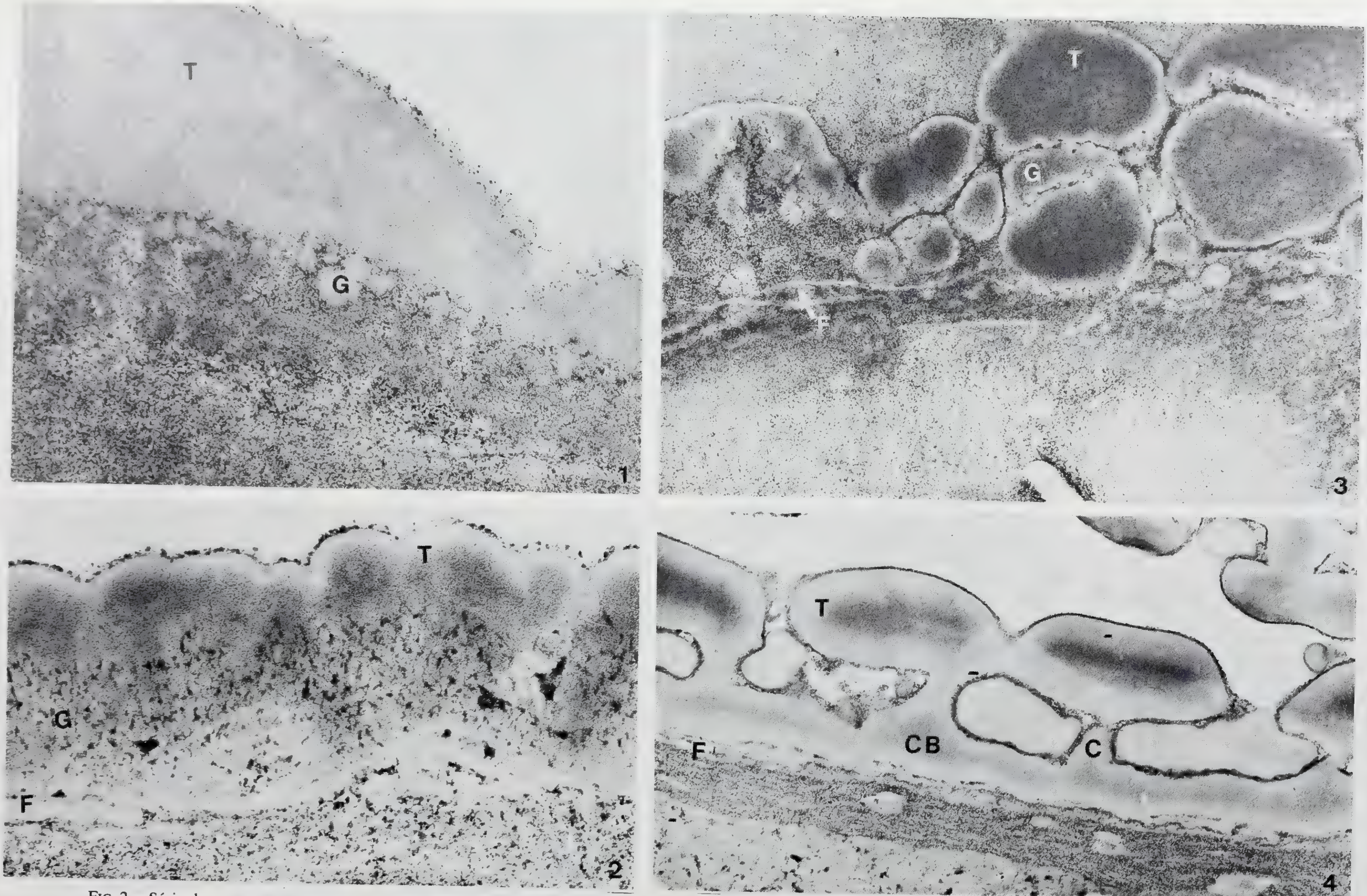

FIG. 2.—Série des structures exiniques du pollen de *Polyalthia*. 1, *P. stuhlmanii*, × 75 000, exine à 2 couches, tectum et couche grenue peu différenciée; 2, *P. suaveolens*, × 50 000, 3 couches, tectum, couche grenue peu différenciée et feuillet (F); 3, *P. longifolia*, × 40 000, 3 couches, tectum verruqueux, couche grenue à grains superposés et feuillets lamellaires; 4, *P. capuronii*, × 24 000, 3 couches, tectum perforé, columelles et couche basale presque entièrement massive. (MET, B. Lugardon, Lab. Biol. Végétale, Toulouse.)

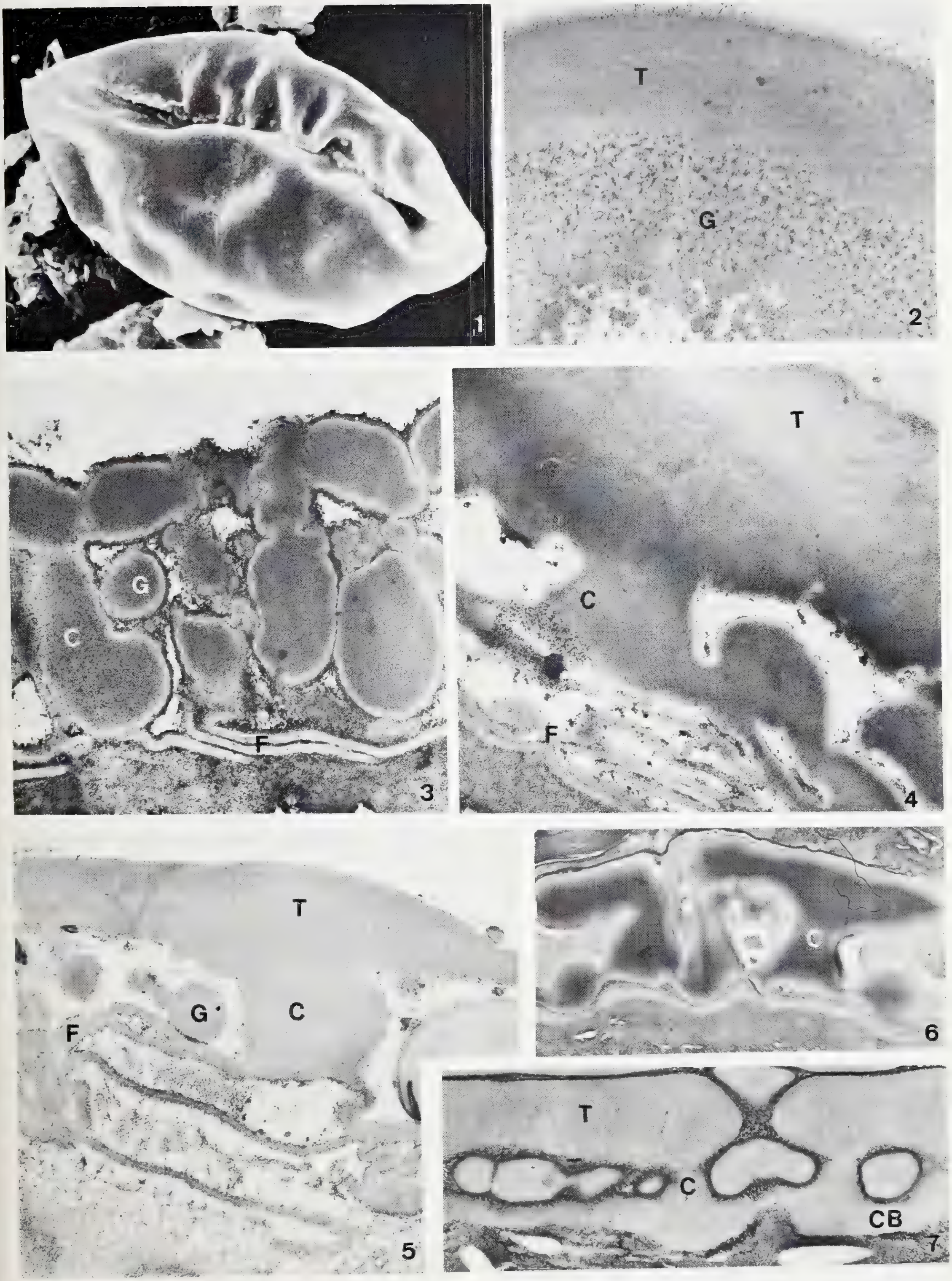

FIG. 3.—1 & 2, *Piptostigma calophyllum*, type pollinique le plus primitif chez les Annonaceae: 1, pollen au MEB, × 2 000; 2, structure de l'exine, pas d'endexine, deux couches, tectum lisse microperforé, et couche grenue très peu différenciée, × 75 000. 3, *Isolona hexaloba*, structure mixte de l'exine, columelles et grains, couche basale feuilletée lamellaire, × 50 000. 4, *Monodora myristica*, structure columellaire avec couche basale feuilletée, × 35 000. 5, *Uvariopsis congolana*, structure mixte, columelles et grains, et couche basale feuilletée, × 25 000. 6, *Dennettia tripetala*, structure columellaire avec couche basale feuilletée, × 15 000. 7, *Enantia chlorantha*, structure columellaire avec couche basale massive, × 35 000. (MET, B. Lugardon, Lab. Biol. Végétale, Toulouse.)

1. Dans deux de ces séries, l'exine conserve une structure primitive, infratectale grenue, sans couche basale feuilletée lamellaire: la première, ou série des *Xylopia,* ayant d'abord conservé son sillon *(Polyceratocarpus, Meiocarpidium)* aboutit à des tétrades lâches inaperturées (*Xylopia, Cananga*) à couche basale massive se fusionnant avec le tectum pour redonner secondairement une exine compacte chez *Neostenanthera* et *Boutiquea*; la seconde, ou série des *Monanthotaxis,* perd très tôt son sillon et est caractérisée par de petits pollens simples inaperturés, échinulés, de type Lauracées.

2. Les deux autres séries sont au contraire marquées par une différenciation de l'exine qui aboutit au type de structure columellaire le plus avancé dans la famille. Dans la série *Polyalthia,* le type pollinique sulqué reste constant, alors que l'on peut observer toutes les étapes de différenciation de l'exine (*Lettowianthus, Cleistopholis, Cleistochlamys, Artabotrys, Enantia*). La dernière série ou série des *Annona,* est en fait celle qui représente l'ensemble de l'évolution du pollen de la famille. Jalonnée par toutes les étapes de différenciation de l'exine dans de nombreux genres, elle est en outre caractérisée par la perte de l'aperture, apparemment survenue très tôt (*Uvaria*), et l'élaboration du type pollinique en tétrade columellaire (*Annona*). Le genre *Isolona* marque une forme de transition particulièrement remarquable dans cette série, puisqu'il traduit à lui seul le passage entre la structure grenue et columellaire, et le type simple inaperturé et composé.

Ainsi, l'évolution du pollen ne peut être interprétée par de simples différences ou ressemblances entre les caractères, mais par une série de caractéres dont on a pu établir les liens de façon continue. De telles series permettent alors d'éviter des rapprochements par simples formes de convergence, ou au contraire, d'établir des liens phylogéniques entre des formes ou des structures différentes.

SIGNIFICATION DES CARACTÈRES DU POLLEN DANS LA PHYLOGÉNIE DES ANNONACEAE

Si certaines tendances générales de l'évolution sont relativement faciles à reconnaître dans la famille, et ont pu être utilisées pour établir des corrélations avec les caractères du pollen, en revanche, il n'est pas toujours facile de saisir le processus selon lequel l'évolution s'est faite dans l'ensemble des taxons. Les séries polliniques permettent de mettre en évidence certains phénomènes de cette évolution.

Réduction de la corolle

Si on l'examine cette fois, en corrélation avec les séries polliniques établies, on remarque que, dans chacune d'elles, se manifeste la même tendance à la réduction des pétales, exprimée de façon parallèle, dans les lignées avec ou sans réduction. Le plus souvent, on la retrouve exprimée par des stades de transition dans chaque phylum, et déjà dans le genre *Piptostigma,* ce qui permettrait de supposer que cette réduction des pétales s'est développée relativement tôt au cours le l'évolution de la famille.

Dans la série des tétrades à structure grenue, il existe deux lignées parallèles, l'une sans réduction correspondant aux structures exiniques les moins évoluées (*Xylopia, Cananga*), l'autre avec réduction incomplète du cycle interne correspondant à la structure exinique compacte secondairement, la plus évoluée (*Neostenanthera, Boutiquea*).

Dans la série *Polyalthia,* le stade de transition que l'on observe déjà chez *Piptostigma* avec un cycle externe réduit, se réalise pleinement chez *Enantia* qui repreésente, par sa structure, le type pollinique le plus avancé de cette série. En revanche, le genre *Polyalthia* ne montre aucune tendance à la réduction des pétales, ce qui semblerait confirmer l'idée de Sinclair (1955) qui voyait dans ce genre un représentant très ancien de la famille des Annonacées et le plus primitif de la tribu des Unoneae.

Les deux autres séries montrent deux modes de réduction parallèles, l'un dans le cycle interne, l'autre par soudure en un seul cycle et disparition d'un pétale de chaque cycle. Dans la série des *Monanthotaxis* (Verdcourt, 1971), ces deux modes ne sont représentés que par des stades de transition et correspondent d'ailleurs à des pollens encore relativement primitifs. Par contre, ils sont pleinement réalisés chez *Dennettia* et *Uvariopsis,* dans la série des types polliniques composés inaperturés, columellaires, les plus avancés.

Les corrélations avec les séries polliniques montrent ainsi qu'il existe, dans chaque phylum, la même tendance qui s'exprime dans des lignées parallèles et souligne d'autre part la diversité des niveaux d'évolution entre les différents caractères.

Les ovules

On distinque dans la famille deux groupes génériques: l'un dans lequel les carpelles ont de nombreux ovules disposés sur deux rangées, l'autre où ils ne renferment jamais qu'un ou deux ovules. Ce caractère n'a guère retenu l'attention des botanistes dans les grandes coupures taxonomiques de la famille. Pourtant, on voit que, dans chacune des séries polliniques, au type de pollen le plus primitif, correspondent des carpelles avec de nombreux ovules. Comme pour la corolle, il se dégage dans chaque série des lignées évolutives dans lesquelles les taxons ont des carpelles renfermant un grand nombre d'ovules, et d'autres où ils n'ont qu'un ou deux ovules. Mais il n'existe, semble-t-il aucun lien privilégié entre l'une ou l'autre de ces lignées et le type pollinique ou la structure exinique. Les pollens composés eux-mêmes peuvent être associés à des lignées pluri ou uniovulées (séries *Xylopia, Annona*).

Cependant les séries polliniques permettent de souligner une tendance générale de l'évolution dans la famille, vers une réduction des ovules à partir de types carpellaires pluriovulés, associés aux types polliniques les plus primitifs.

Syncarpie multiloculaire et vraie syncarpie

Dans quelques genres d'Annonacées, les carpelles, libres dans la fleur, sont plus ou moins soudés dans le fruit, pouvant même consituer un véritable syncarpe à nombreuses loges (*Annona, Anonidium*).

C'est une étape biologique importante puisqu'en devenant plus gros, charnus, juteux, ces fruits deviennent de plus en plus attractifs pour les animaux frugivores qui assurent secondairement une dispersion efficace des graines. On pourrait même penser qu'ils constituent une étape évolutive vers le vrai syncarpe (*Isolona, Monodora*) qui provient du développement d'un ovaire unique à placentation pariétale.

En réalité, on constate que le syncarpe pluriloculaire apparaît à des niveaux très variés dans trois séries polliniques (*Boutiquea–Letestudoxa, Anonidium* et *Annona–Pachypodanthium*), à l'exception de la série *Polyalthia* où le pollen conserve son sillon. Si, comme pour les ovules, il ne se trouve associé à aucun type de structure exinique privilégié, on remarque cependant qu'il correspond toujours à des types polliniques inaperturés, donc plus évolués, et à des lignées parallèles dans lesquelles il y a réduction d'ovules. L'ovule unique, dressé au fond de la loge ovarienne, plus ou moins immergée dans le réceptacle, apparaît donc comme une tendance évolutive secondaire.

En revanche, la syncarpie uniloculaire, ou vraie syncarpie, des genres *Isolona* et *Monodora* représente apparemment l'expression d'une mutation brutale du carpelle pluriovulaire.

CONCLUSION

Pris isolément, les caractères du pollen des Annonacées auraient pu conduire à rapprocher certains taxons éloignés tels que *Xylopia* ou *Annona*, par exemple, ou, au contraire à en scinder d'autres très homogènes comme *Polyalthia*. En revanche, si l'on utilise les séries morphologiques continues, témoignant de l'évolution même du caractère pollinique, on s'aperçoit qu'elles permettent de mettre en relief certaines manifestations de l'évolution, non visibles dans les classifications existantes, et qu'elles tendent à montrer que la fleur des Annonacées est une structure en voie de réduction.

Si, d'autre part, la différenciation des caractères, tels qu'on les perçoit en les mettant en corrélation avec ceux du pollen, montre un parallélisme remarquable dans chaque série, elle souligne nettement qu'ils ne varient pas nécessairement ensemble. Les multiples essais disjoints, la plupart du temps sans devenier consituent une véritable mosaïque des niveaux d'évolution.

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The endothecium — a neglected criterion in taxonomy and phylogeny?

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ABSTRACT

A method has been devised for the screening of the endothecium in flowering plants, principally with a view to describing the cell wall thickening. A scheme of nomenclature and coding has been proposed, which permits a more detailed and unambiguous recording of endothecial variety than was hitherto possible. There is some evidence that this structural variation could have taxonomic and phylogenetic significance.

RÉSUMÉ

L'ENDOTHÉCIUM, UN CRITÈRE NÉGLIGÉ EN TAXONOMIE ET PHYLOGÉNIE?

Une méthode d'observation détaillée de l'endothécium chez les phanérogames a été établie, principalement en vue de décrire l'épaissisement de la cloison cellulaire. L'établissement d'une terminologie et d'une codification, qui permet de distinguer la variation de l'endothécium de façon plus détaillée et moins ambiguë que jusqu'à présent, a été proposé. Il semble que cette variation structurale pourrait avoir une portée taxonomique et phylogénétique.

The study of anther structure has for a long time been overshadowed by the considerable advances in systematic and historical palynology and by the more recent work on the biology of the tapetum and pollen. Although there have been numerous applications of the external morphology of the stamen to taxonomic problems, the wealth of variety in anther wall histology is still incompletely explored or exploited.

One such source of variety is the structure of the mature endothecium, the so-called hypodermal fibrous layer. The most comprehensive studies of the characteristic wall thickening patterns in this tissue were made by Purkinje (1830), Chatin (1870), Le Clerc du Sablon (1885) and Kuhn (1908). Kuhn appreciated the need to consider the three dimensional aspects of the endothecial cell and identified six cell types on a basis of their wall thickening. The value of the endothecium in taxonomy was investigated by Dormer (1962) and Nordenstam (1978), with reference to the Asteraceae, by Arora & Tiagi (1977) in the Apiaceae and by Eyde (1977) in the Onagraceae. In these families wall thickening patterns were shown to have some diagnostic potential. Nevertheless, Davis (1966) had concluded that the endothecium appeared to have no taxonomic value, although in her extensive review she usually recorded only whether 'fibrous' thickenings were present or not.

It is the intention of this contribution to show that the range of structural diversity in the endothecium is much greater than was previously described. A comprehensive system of description and nomenclature will be developed in order that the systematic potential of endothecial features can be better assessed.

MATERIALS AND METHODS

Preparations of the endothecium were made from both fresh material stored in formalin-propionic-acetic acid or 70% ethanol, and from dried herbarium specimens. Voucher specimens are preserved at the Natal University Herbarium (NU) in Pietermaritzburg, together with pickled material. So far over five hundred taxa have been examined.

Mature stamens were maintained for 15 mins in 60% aqueous lactic acid at 95° C. They were then mounted on a slide in glycerine jelly after opening the loculi and flattening the walls. A varying degree of maceration took place: sometimes the epidermis was removable in a sheet and often the endothecial cells were readily separable. Some large anthers, such as *Bruguiera gymnorrhiza* (L.) Lam. required up to 2 hrs heating. Herbarium material may need preliminary boiling in water, although this was not usually necessary. The samples described were from the central region of the loculus wall: the connective and specialized areas such as the stomium were not included.

The wall thickenings were examined and photographed with Nomarski interference contrast optics in a Reichert Univar microscope.

GENERAL FEATURES OF THE ENDOTHECIUM

It is not proposed to consider the development or homology of the fibrous layer: this has been done by Eames (1961) and Davis (1966). It is sufficient to point out that the wall of the anther loculae varies in thickness and complexity, but that in most species at maturity comprises only an epidermis and endothecium, the ephemeral middle layers and tapetum making no effective contribution. The endothecial cells may be more or less isodiametric, broadly fusiform or elongated to varying degrees, and lying paralleled or normal to the epidermal surface. The orientation is usually related in a specific way to the long axis of the anther. There is a considerable range in cell size, the tangential width in *Euphorbia hirta* L. and *Plectranthus laxiflorus* Benth. being only 10,0

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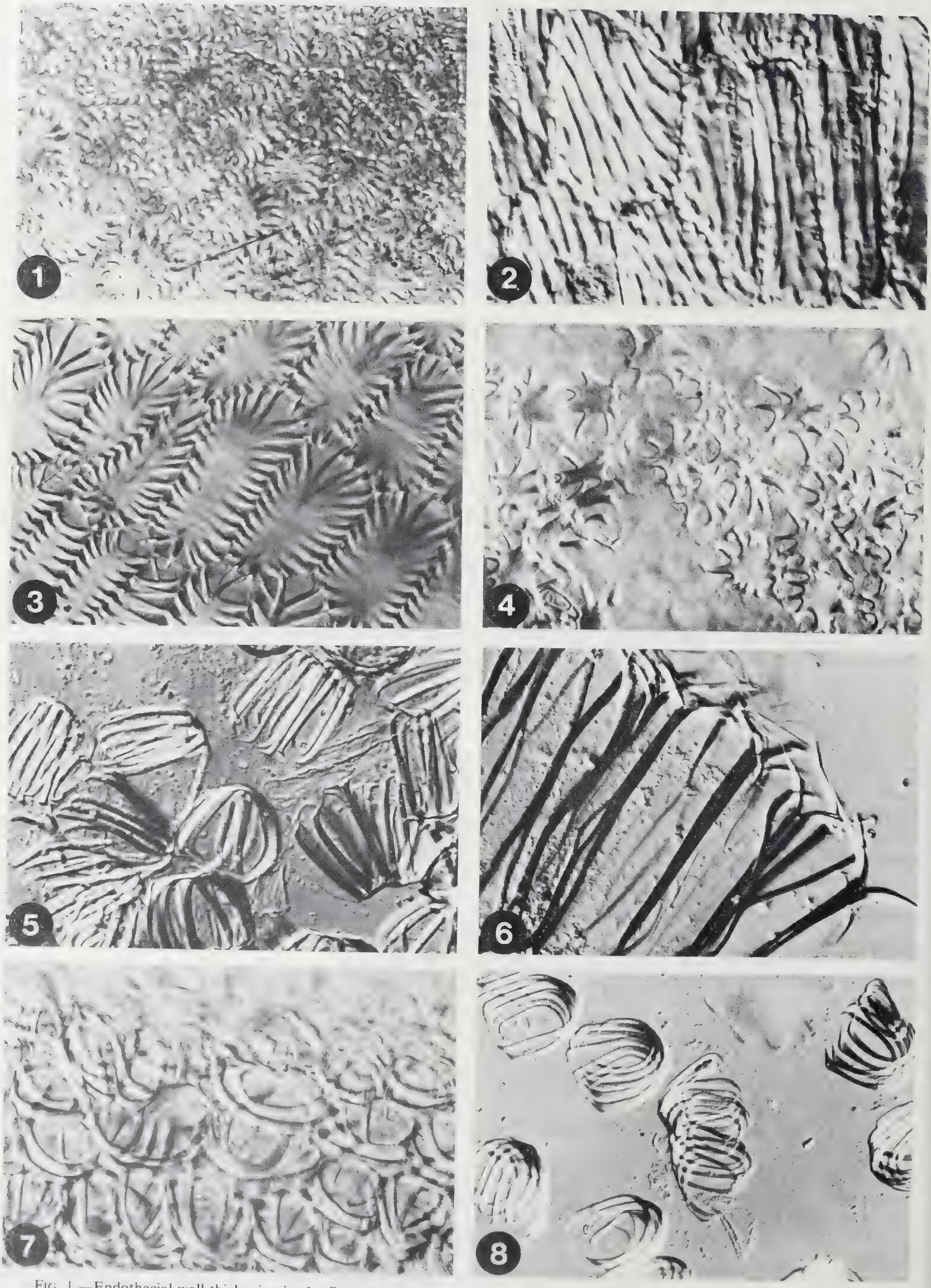

FIG. 1.—Endothecial wall thickening in: 1, *Commicarpus plumbagineus;* 2, *Ochna natalitia;* 3, *Burnatia enneandra;* 4, *Valeriana capensis;* 5, *Polygala virgata;* 6, *Lilium candidum;* 7, *Hermannia gerrardii;* 8, *Cephalalaria natalensis;* (all × 800).

and 12,5 μm respectively, whereas that of *Tradescantia virginiana* L. was found to exceed 100 μm.

CELL WALL THICKENING

The few studies that have been made of the development of the characteristic wall thickenings (Heslop-Harrison, 1968; De Vaal, 1978) indicate that secondary, orientated cellulose deposition takes place in a manner very similar to that which occurs during the differentiation of primary xylem elements. It is interesting to note that when no secondary wall deposition takes place, such as in *Erica oatesii* Rolfe, *Galopina circaeoides* Thunb. and *Philippia evansii* N.E. Br., all walls are quite thin. When thickening does occur, it is usually highly localized, in a pattern representing a high degree of specific organization. Only rarely are all walls equally and heavily thickened: one example is in the giant anthers of *Hydnora solmsiana* Dinter. Another uncommon type, where all walls show heavy reticulate thickening, occurs in *Chironia baccifera* L.

It is convenient to consider these thickenings in isolation from the rest of the wall and cell of which they are a part, admittedly an artificial approach. It then becomes possible to identify patterns of thickening and to recognize the components of variety, to which can be ascribed a name and a numerical code. For example, the inner tangential cell wall alone may be completely and heavily thickened or, alternatively, the thickening may be restricted to more or less of the centre of the wall. This thickening may be termed the 'base plate'. The presence of circular or lenticular unthickened regions characterize a 'perforate' plate, e.g. *Commicarpus plumbagineus* (Cav.) Stanl. (Fig. 1.1), *Ochna natalitia* (Meisn.) Walp. (Fig. 1.2) and *Clematis brachiata* Thunb. Absence of continuous thickening from around the margins of the tangential wall, so that the plate appears suspended, can be designated tympanate (*Burnatia enneandra* Micheli, Fig. 1.3) or with still further reduction, in isodiametric cells, palmate (*Valeriana capensis* Thunb., Fig. 1.4) and in elongate cells, rachial. The plate may eventually consist of no more than an anastomosis of strands running into the anticlinal walls. In an entirely different kind of thickening, 'polygonal', only the rims of the tangential walls are affected and the more or less angular rings of adjacent cells lie edge to edge to form a net. At least 11 states of the feature 'base plate' may be distinguished, the 300 series in Table 1. This tangential view of the endothecial cells is the most readily observed, and the thickening pattern, in conjunction with cell size and shape shows a large amount of potentially useful variation.

Thickening of the anticlinal walls usually takes the form of riblike extensions of the base plate. Diversity arises from the number, spacing, thickness and cross sectional profile (round to D shaped, as opposed to being obviously flattened). The ribs vary in length, in *Pelargonium luridum* (Andrs.) Sw. consisting of little more than triangular teeth fringing the plate. Alternatively the ribs fork and join to make a stout reticulum. In some more or less symmetrical cells the ribs seem to arise from radiate thickenings of a large, thin, somewhat scalloped plate, giving a very characteristic type which may be called 'foliate', as in *Crinum moorei* Hook. f. The opposite extreme is represented by the lobster pot or ptenoid type in *Polygala virgata* Thunb. (Fig. 1.5), in which the symmetrical cell is enclosed by a cage of strands originating in a basal plexus and curving over to partially reinforce the outer tangential wall.

An interesting feature is the mode of termination of the ribs, either at the junction of the anticlinal wall with the outer tangential wall, or after turning across this outer wall. If the ribs are confined to the anticlinal wall, they may end in a flat top with pointed extensions on each side, the 'serif' type as shown by *Lilium candidum* L. (Fig. 1.6). If the ribs are very closely spaced, accentuated serifs can join laterally, forming in effect the rim of a basket, such as in *Hermannia gerrardii* Harv. (Fig. 1.7). Three variants 'sans-serif' are possible, rounded, knobbed or tapered to a point. The extent to which the ribs continue across the outer tangential wall varies from a slight incurving, when the centre region of the wall is left unsupported, to a complete traverse and even continuation down the opposite side of the cell.

The absence of continuous thickening of the inner tangential wall, that is the absence of base plate, has a profound effect on the pattern, and presumably mechanical consequences, of the thickening of the rest of the cell. The simplest and commonest of these patterns consists of a series of unconnected U-bars, involving the inner tangential and anticlinal walls only (*Cephalaria natalensis* Kuntze, Fig. 1.8). The profile of the U may be sharply angular or rounded, wide with relatively short ribs or narrow, with long ribs. These ribs show the same variety of ending as described previously: they may also show more or less regular branching, the effect of which is that the outer tangential wall may have many more ribs or rib endings than does the inner tangential wall. If one, or even both of the ribs of a U continues across the outer tangential wall and down the opposite side of the cell, without joining the ascending ribs on that side, a pseudo-annular pattern results, as exemplified by *Diclis rotundifolia* (Hiern) Hilliard & Burtt, *Oenothera biennis* L. (Fig. 2.1), *Oxalis semiloba* Sond. or *Wahlenbergia zeyheri* Eckl. & Zeyh. Two further important related types are 'annular', with true rings (*Ipomoea ficifolia* Lindl., Fig. 2.2) and 'helical' (*Acalypha peduncularis* E. Mey., Fig. 2.3, and *Rinorea natalensis* Engl., Fig. 2.4). Helically thickened cells vary greatly in size, shape, number of gyres and strand thickness, and may even show double or opposed helices. The ends of the helix may be closed by spiral reinforcement of the anticlinal walls (*Aloe kraussii* Bak., Fig. 2.5). Although the names are self explanatory, considerable care is needed in practice, to discriminate between these plateless types of thickening. This is not difficult if maceration has effectively isolated the cells, but may be so with an intransigent endothecium overlain by a thickened epidermis. Furthermore, cells with pseudo-annular, annular and helical thickening, can intergrade locally, so that one may encounter a short helical section within an annularly thickened cell.

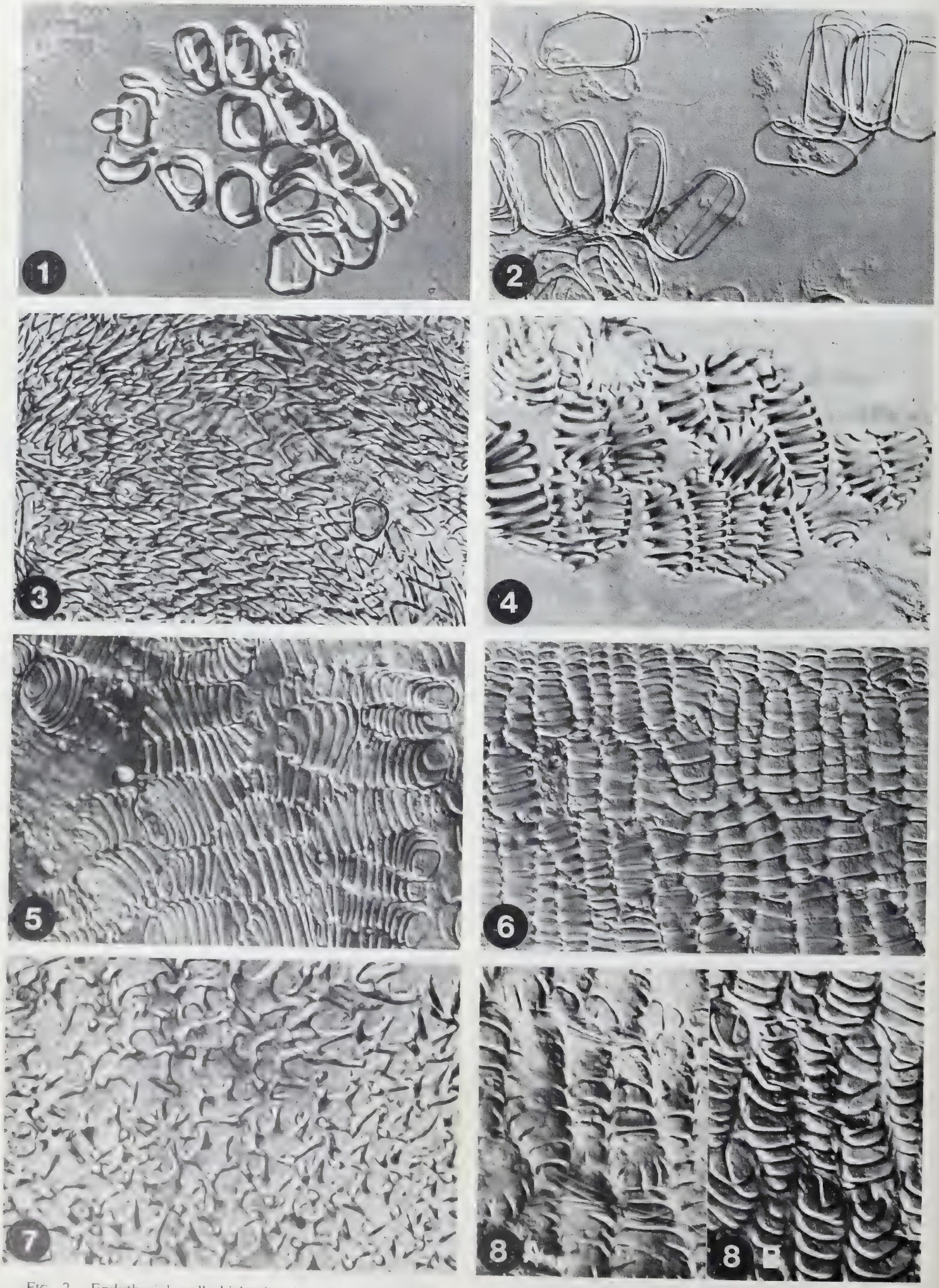

FIG. 2.—Endothecial wall thickening in: 1, *Oenothera biennis*, 2, *Ipomoea ficifolia;* 3, *Acalypha peduncularis;* 4, *Rinorea natalensis;* 5, *Aloe kraussii;* 6, *Piper capense;* 7, *Rorippa nasturtium-aquaticum;* 8, *Dianthus basuticus*—a, inner tangential and b, outer tangential views of the same field; (all × 800).

TABLE 1.—Summary and coding of endothecial characters

Cell character	Numerical code and character state				
Cell size[1]	111 Large: > 75 µm	112 Medium 25–75 µm	113 Small: < 25 µm		
Shape	121 ± Isodiametric	122 Rectangular	123 Fusiform	124 Vertical	
Wall thickening	201 Absent	202 Present: all walls solid	203 Present: all walls reticulate	204 Present: localized	
Base plate	311 Absent	312 Thin	313 Thick		
Proportion	321 Entire	322 > ½ (Tympanate)	323 < ½ (Palmate or rachial)	324 Anastomosis	325 Polygonal
Perforation	331 Imperforate	332 Small and few	333 Large		
Ribs: Pattern	411 U	412 Pseudo-annular	413 Annular	414 Helical	415 Doubly Helical
No per cell	421 < 6	422 > 5 < 14	423 > 14		
Spacing	431 Wide (> twice rib width)	432 Close (< twice rib width)			
Branching	441 Absent	442 Present			
Length	451 Short (< ⅔ cell height)	452 Long (> ⅔ cell height)	453 Overtopping		
Profile[2]	461 Angular	462 Rounded			
Section[2]	471 D to round	472 Flattened	473 Thin, tapering		
Tip	481 Serif	482 Rounded	483 Knobbed	484 Pointed	

[1] Length in tangential view
[2] In rib or ring

TISSUE PATTERNS

The cell wall features described above contribute to an overall tissue pattern, which in a preparation of an extensive area of the loculus wall may be very striking, and for some purposes, sufficiently diagnostic. For these a separate set of descriptions may be applied, such as 'daisy field' for the small palmate pattern of *Piper capense* L. (Fig. 2.6) or 'scalariform' the pattern in *Rorippa nasturtium-aquaticum* (L.) Hayek (Fig. 2.7). Usually there will be an inner and an outer tangential view which differ considerably from one another, as in *Dianthus basuticus* Burtt Davy (Fig. 2.8 A & B.) However, these patterns are not sufficiently sensitive and each can be derived from more than one cell type. There are also a number of other features which can be recorded from the same preparation, such as the presence of druses, wall thickening in the connective and in the epidermis, and cuticular sculpturing but these are insufficiently explored.

CONCLUSIONS

Table 1 summarises the variation in endothecial wall thickenings so far recognized. It incorporates a code, so that the aggregate states of this feature can readily be scored for a large sample of taxa. Although this scheme is tentative, it is nevertheless clear that much more structural variety exists than has been reported previously and that it is susceptible to systematic description. The illustrations of Kuhn (1908) and other early writers were too diagrammatic and in numerous subsequent contributions to plant embryology, even where anther development has been described and figured, the endothecial wall thickenings have usually been inadequately represented. It is known (De Vaal, 1978) that the wall thickenings attain their final form only late in the development of the anther, and it is possible that many stylized illustrations were based on immature cells.

The observations described here are presented as material for a study of structural variation: it is premature to comment on their taxonomic and phylogenetic significance. There are indications of constancy at the generic level, or even through larger groups such as the Asteraceae. There is also a discernible trend of the presence of a base plate and heavy lateral thickening through the Magnoliidae and Ranunculidae (*sensu* Takhtajan), a view which corroborates that of Eyde (1977). It is also apparent that a connection between endothecial type and anther function is less direct than might be anticipated.

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The morphology and systematic position of the Didiereaceae of Madagascar

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ABSTRACT

The Didiereaceae, endemic to the arid south-west of Madagascar is one of the most remarkable plant families in the world. Four genera and 11 species are known, of which 3 have been described by the author: *Decaryia* (1 species), *Alluaudiopsis* (2 spp.), *Alluaudia* (6 spp.) and *Didierea* (2 spp.). The species show different growth forms, but their shoot-stem-systems are basically similar; they are all spiny, semi-succulent deciduous shrubs or trees, with a stem (shoot) system differentiated into long-shoots and short-shoots (brachyblasts). The long shoots bear normal leaflets, which soon fall off. In their axils, brachyblasts develop proleptically, which produce two types of leaves (1) thorns which develop proleptically in different numbers (1 in *Alluaudia,* 2 in *Alluaudiopsis marnieriana* and several *Didierea*); (2) leaves which are green, deciduous assimilation organs (2 per brachyblast in *Alluaudia,* several in *Didierea).*

The stem organization is comparable to that of the Cactaceae of the New World. The brachyblasts of the Didiereaceae are homologous to the areoles of the Cactaceae, most obviously to those of the primitive members, the Pereskioideae. The affinities between the two families can be demonstrated by means of grafting. It is possible to graft Didiereas onto Pereskioideae and vice versa.

The flower structure of Didiereaceae is very uniform. Flowers are unisexual and dioecious and show affinities to those of the Portulacaceae. The development of the gynoecium, the ovule and the female gametophyte as well as the presence of betalains in the flowers indicate that the Didiereaceae do not belong to the Sapindales as was sometimes assumed, but to the Centrospermae. They should be placed between Portulacaceae and Cactaceae. The ancestors of the Didiereaceae are not known.

RÉSUMÉ

LA MORPHOLOGIE ET LA POSITION SYSTÉMATIQUE DES DIDIÉRÉACÉES DE MADAGASCAR

Les Didiéreacées, endémiques dans le sud-ouest de Madagascar, sont une des familles de plantes les plus remarquables du monde. Quatre genres et onze espèces sont connus, dont trois ont été décrites par l'auteur: Decaryia *(1 espèce),* Alluaudiopsis *(2 spp.),* Alluaudia *(6 spp. et* Didierea *(2 spp.). Les espèces montrent des formes biologiques différentes mais leurs systèmes de ramification sont fondamentalement similaires: ce sont tous des arbres ou arbustes décidus, épineux, semi-succulents, avec un système de ramification différencié en rameaux longs et rameaux courts (brachyblastes). Les rameaux longs portent de petites feuilles normales qui tombent très vite. A leur aisselle, des brachyblastes se développent proleptiquement et produisent deux types de feuilles (1) des épines qui se développent proleptiquement en nombres divers (1 chez* Alluaudia, *2 chez* Alluaudiopsis marnieriana *et plusieurs chez* Didierea*); (2) des feuilles qui sont des organes d'assimilation verts et caducs (2 par brachyblaste chez* Alluaudia *et plusieurs chez* Didierea).

L'organisation de la tige est comparable à celle des Cactacées du Nouveau Monde. Les brachyblastes des Didiéréacées sont homologues aux aréoles des Cactacées, de manière plus évidente à celles de ses membres primitifs, les Pereskioïdées. Les affinités entre les deux familles peuvent être démontrées au moyen du greffage. Il est possible de greffer des Didierea *sur des Pereskioïdées et vice-versa.*

La structure florale des Didiéréacées est très uniforme. Les fleurs sont unisexuées et dioïques et montrent des affinités avec celles des Portulacacées. Le développement du gynécée, de l'ovule et du gamétophyte femelle aussi bien que la présence de bétalaïnes dans les fleurs indiquent que les Didiéréacées n'appartiennent pas aux Sapindales comme cela fut quelquefois supposé, mais aux Centrospermées. Elles devraient être placées entre les Portulacacées et les Cactacées. Les ancêtres des Didiéréacées ne sont pas connus.

One of the most remarkable groups of flowering plants are the Madagascan Didiereaceae, one of the seven endemic families of the 'Grand Ile.' They are not only characterized by an unusual morphology, but their precise systematic position has not been finally established. As regards geographical distribution, the members of this small family are restricted to a limited area, viz. the coastal region of the extreme dry south-west of the Island (Fig. 1). We know nothing of their ancestry or affinities, neither in Madagascar itself nor in neighbouring Africa and other parts of the world. In the extreme south-west, the Didiereaceae are associated with arborescent leafless, more or less succulent Euphorbias such as *Euphorbia enterophora, E. stenoclada, E. leucadendron, E. plagiantha* and others. Together they form a deciduous plant community, known as *Euphorbia*-Didiereaceae Bush (Fig. 2). Four genera of the Didiereaceae with 11 species are presently recognized, three of which have been described by the author. The genera, mostly named after French generals, are the following: *Decaryia* (monotypic: *D. madagascariensis*), *Alluaudiopsis* (two species: *A. fiherenensis* and *A. marnieriana*), *Alluaudia* (six species: *A. procera, A. montagnacii, A. ascendens, A. comosa, A. dumosa* and *A. humbertii*) and *Didierea* itself (two species: *D. madagascariensis* and *D. trollii*). All are woody succulents, shrubs or

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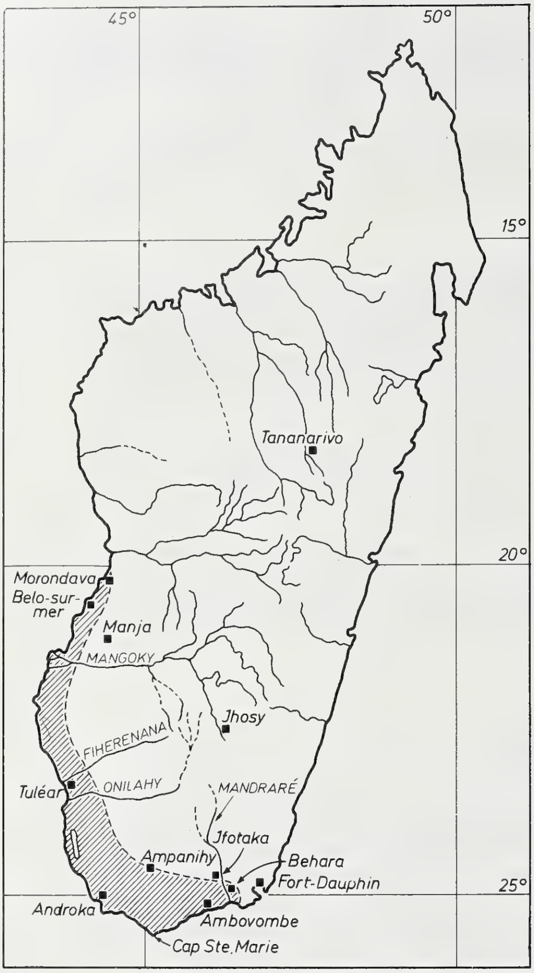

FIG. 1.—Distribution of *Euphorbia* – Didiereaceae Bush (hatched) in Madagascar.

trees, up to 15 m high, but the arborescent species pass through a shrubby juvenile stage. The best example showing the different stages is *D. trollii.* Early on the plant forms a 'thicket' of creeping, plagiotropic shoots; with increasing age, one (or more) shoot(s) start to grow upright, forming trunks, which later branch, forming a crown, while the basal branches die off (Fig. 3). Most of the Didiereaceae are of arborescent growth; only *Alluaudiopsis* retains a shrubby growth-form.

All Didiereaceae are spiny plants and show a sharp differentiation between long-shoots and short-shoots (brachyblasts). In other words, the Didiereaceae have the same organization as the primitive Cacti, *Pereskia* and *Pereskiopsis:* the short-shoots have an extremely short axis which, in most species, is buried into the cortex; only in *Didierea* is the growing point of the short-shoots elevated on a more or less elongated podarium (Fig. 4), as for example in genus *Leuchtenbergia* of the Cactaceae. The brachyblasts of the Didiereaceae are homologous to the areoles of the Cacti; they develop proleptically in the axils of normal, but soon deciduous long-shoot leaves; they produce, also proleptically, thorns, which correspond to those of the Cacti (representing transformed leaves); in each growing period the areoles produce leaves as assimilation organs, as can be observed sometimes in the areoles of the primitive Cacti; also, the inflorescences descend from the areoles and an areole can be transformed into a long-shoot. It is surprising that French botanists such as Choux, Perrier de la Bathie and Humbert did not recognize this organization.

The thorns appear in different numbers and positions in the different genera: in *Decaryia* and *Alluaudiopsis marnieriana* there are two thorns in a lateral position occurring as stipules (the same structure exists in *Pereskia aculeata*); in *Alluaudia* (adult plants) only one brachyblast-thorn is formed; it stands in a median position above the areole-growing point; in *Didierea* the thorns are arranged in whorls of mostly four, and the median-basal-one is often elongated.

Differences also exist in the number of the brachyblast-leaves in the different genera. *Alluaudia dumosa* is mostly leafless throughout the year; in the other species the leaves are produced mostly in pairs, and the shortly petioled lamina takes a vertical position, so that a long-shoot, fully covered with leaves, looks very strange (Fig. 5); in *Didierea,* the small and narrow-lanceolate brachyblast-leaves appear in great numbers in the form of rosettes.

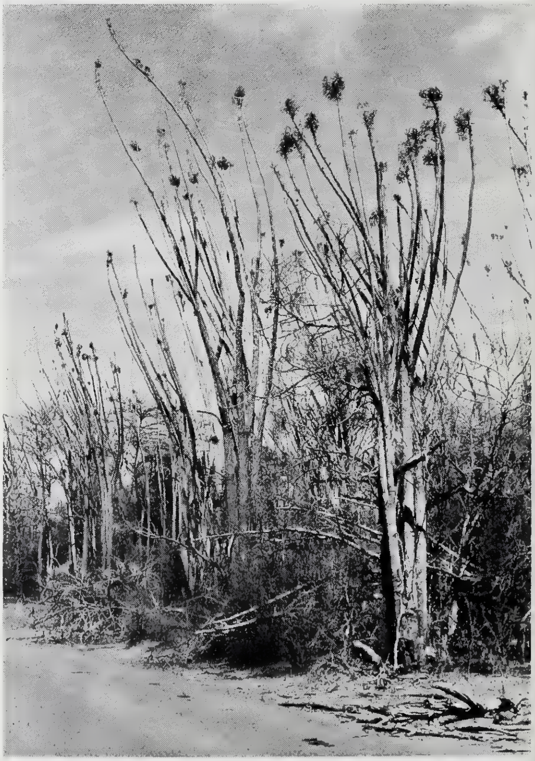

FIG. 2.—*Euphorbia* – Didiereaceae Bush with flowering plants of *Alluaudia procera* near Ampanihy, S. W. Madagascar.

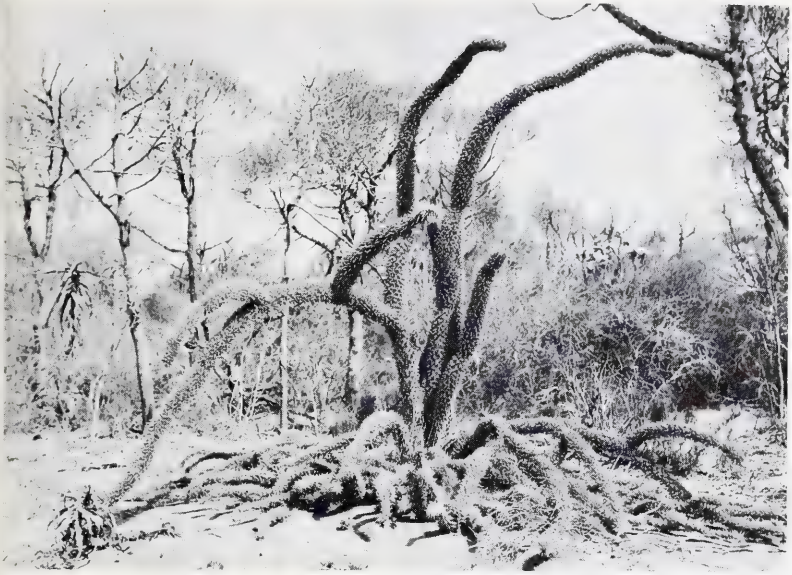

FIG. 3.—*Didierea trollii* with several trunks and dying basal branches.

These brachyblast-leaves are the true assimilatory organs; they persist during the rainy season and die off at the beginning of the dry period; but the same areole is able to form new leaves in the next growing season.

It is clear that the primitive-foliaged Cacti and the Didiereaceae show a striking convergence in the organization of their shoots; the inflorescence and flower-structure, however, is quite different in the two families. This may be the reason that the Didiereaceae were not considered as belonging to the Centrospermales, but rather to the Sapindales.

The flowers of the Didiereaceae seldom appear singly: they are arranged in more or less richly branched inflorescences; they appear instead of leaves in a lateral position along the long-shoots, i.e. an areole growing-point can become fertile and produce an inflorescence instead of leaves. In principle, the inflorescences of all species are monotelous synflorescences (in the sense of Troll); the abortion of the terminal flowers of the partial inflorescences leads to so called 'Rumpf-synflorescences' (Troll). *Didierea, Alluaudiopsis marnieriana* (Fig. 6) and *Alluaudia comosa* have extremely reduced inflorescences: only the terminal flower of a dichasium is developed, so that a whole paracladium simulates a single flower. We call these reduced partial inflorescences 'monades'; in *Didierea* many of them appear in one areole at the same time, so that a branch, at flowering-time, is profusely covered with opened flowers (Fig. 7). The length of the synflorescence axis is variable: in most of the *Alluaudia* species it is well developed and can reach a length up to 15 cm; in *Alluaudia comosa, Alluaudiopsis marnieriana* and *Didierea* the axis is so short that the flower-buds are hidden in the groove of the areole. The flowers of all Didiereaceae are dioecious and haplochlamydic. The four tepals are surrounded at the base by two often keeled bracts, which form a kind of involucrum. In the female flowers they enlarge during embryogenesis and serve to distribute the small nut-fruits by wind.

Mostly the Didiereaceae is considered as belonging to the Sapindales. The male flowers have a variable number (6–10) of stamens; the filaments are united at their base to a ring, which produces secretory tissue on its inner side; the pistil is

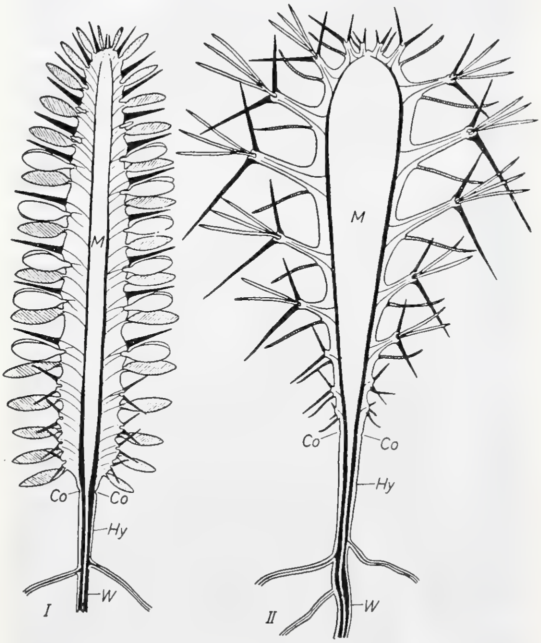

FIG. 4.—Growth form of young plants of *Alluaudia procera* (I) and *Didierea madagascariensis* (II). The leaves of the short-shoots (brachyblasts) are unhatched and those of the long-shoots, hatched. W, main root; Hy, hypocotyl; Co, cotyledons; M, pith.

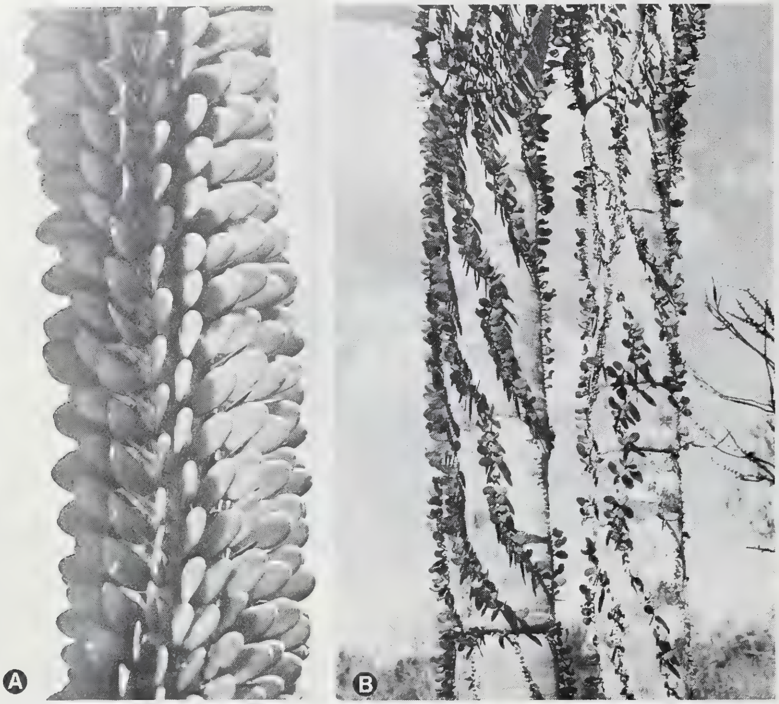

FIG. 5.—*Alluaudia procera*. Stems (a) and long-shoot (b) with the leaves of the brachyblasts. Each growing point produces two vertical leaves.

atrophied and sterile; in the female flowers the stamens are reduced to staminodes; the gynoecium is trimerous, but only the medium-adaxial carpel is fertile and bears one hemicampylotropous ovule. This is bitegmic, and between both integuments, a small split, a special peculiarity of the ovules of the Centrospermae, can be observed. Embryogenesis is of the *Chenopodium*-type; the embryo is campylotropous and embedded in a thin tissue of perisperm.

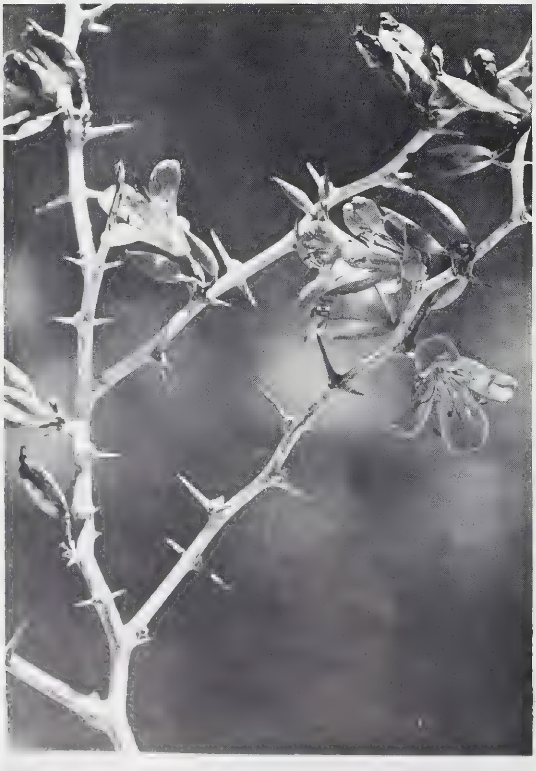

FIG. 6.—*Alluaudiopsis marnieriana*. Branches with male (a) and female (b) flowers.

The systematic position of the Didiereaceae was, for a long time, unclear, but our morphological, anatomical, embryological and biochemical investigations have shown that the Didiereaceae belong, without doubt, to the Centrospermae; the discovery of *Alluaudiopsis marnieriana* by the author provided important proof of this hypothesis. It is the only member of the Didiereaceae with carmine red tepals; in all the other species only the filaments and the well-developed stigmas are red-carmine in colour, but this red colour, as Reznik confirmed, is not caused by normal anthocyans, but by red betaine, a plant colour-substance, which has so far only been found in families of the Centrospermae. This character is one of the main reasons for placing the Didiereaceae in the Centrospermae. The Didiereaceae is a distinct family within the tribe Centrospermae and has relationships with the Portulacaceae and Basellaceae as well as the Cactaceae and Nyctaginaceae. Therefore, we can consider the spiny Didiereaceae as the Cacti of the Old World; both groups have the same organization of their vegetative organs, i.e. differentiation into brachyblasts (= areoles) and long-shoots, and also show reduction of the long-shoot-leaves and the formation of leaf-thorns. Moreover, it is possible to graft Didiereaceae onto Cacti and vice versa a further proof, in our opinion, of the relationship of these two plant-groups.

Unfortunately, we know nothing of the phylogeny of the Didiereaceae. We have not yet found

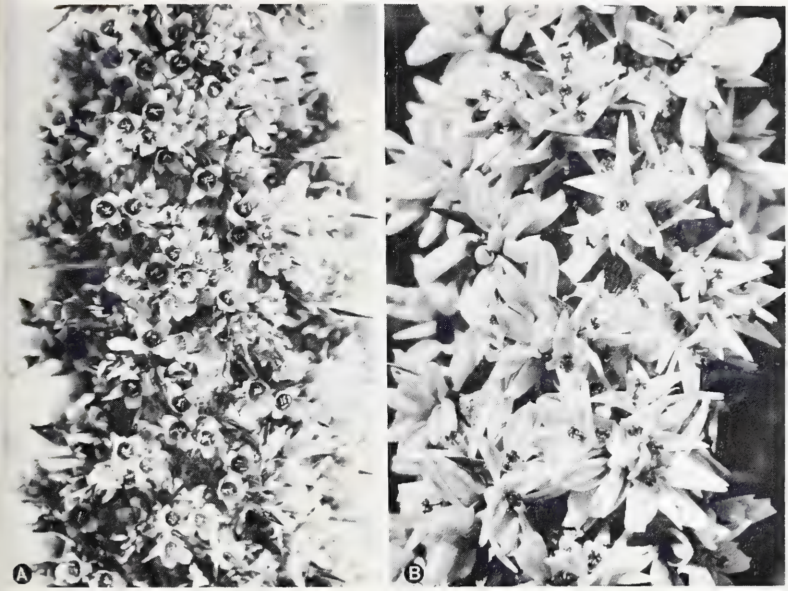

FIG. 7.—*Didierea madagascariensis.* Long-shoot with male flowers (a) and female flowers (b).

plants either in Madagascar itself or in neighbouring Africa and Asia, in which the ancestry of the Didiereaceae could be traced. The family has developed after the isolation of the island from the continent; it is possible that, before the massive destruction of primary vegetation in Madagascar, plants existed which could be regarded as ancestors of this interesting plant group. Unfortunately, no fossils have been found to help elucidate the phylogeny of the Didiereaceae.

Bothalia 14, 3 & 4: 845–848 (1983)

The genus *Capsicum* (Solanaceae) in Africa

W. H. ESHBAUGH*

ABSTRACT

The genus *Capsicum* (Solanaceae) includes approximately 20 wild species and 4–5 domesticated taxa commonly referred to as 'chilies' or 'peppers'. The pre-Colombian distribution of the genus was New World. The evolutionary history of the genus is now envisaged as including three distinct lines leading to the domesticated taxa. The route of *Capsicum* to the Old World is thought to have followed three different courses. First, explorers introduced it to Europe with secondary introduction into Africa via further exploratory expeditions; second, botanical gardens played a major role in introduction; and third, introduction followed the slave trade routes. Today, pepper production in Africa is of two types, vegetable and spice. Statistical profiles on production are difficult to interpret, but the data available indicate that Nigeria, Egypt, Tunisia and Ghana are the leading producers. Production is mainly a local phenomenon and large acreage is seldom devoted to the growing of peppers. The primary peppers in Africa are *C. annuum* and *C. frutescens.*

RÉSUMÉ

LE GENRE CAPSICUM *(SOLANACÉE) EN AFRIQUE*

Le genre Capsicum *(Solanacée) inclut approximativement 20 espèces sauvages et 4–5 taxa domestiqués communément dénommés 'chilies' ou 'peppers'. La répartition pré-Colombienne du genre se situait dans le Nouveau Monde. L'histoire de l'évolution du genre est maintenant envisagée comme incluant trois voies distinctes conduisant aux taxa domestiqués. On pense que la migration des* Capsicum *vers le Vieux Monde a suivi trois voies différentes. En premier lieu, des explorateurs l'introduisirent en Europe, puis de là en Afrique, par le biais d'explorations ultérieures en second lieu, les jardins botaniques jouèrent un rôle majeur dans cette introduction et en troisième lieu, l'introduction suivit les routes de la traite des esclaves. Aujourd' hui, la production de* Capsicum *en Afrique est de deux types: légume et épice. Les données statistiques sur la production sont difficiles à interpréter, mais celles disponibles indiquent que le Nigeria, l'Egypte, la Tunisie et le Ghana sont les principaux producteurs. La production est surtout un phénomène local et il est rare que de larges superficies soient consacrées à la culture des* Capsicum *. Les principaux* Capsicum *en Afrique sont* C. annuum *et* C. frutescens.

Capsicum is a New World genus comprising approximately 20 wild species and 4–5 domesticated taxa (Eshbaugh, 1980a; Table 1). Hunziker (1956) divides the genus into the three sections *Capsicum, Pseudoacnistus* and *Tubocapsicum.* The monotypic section *Tubocapsicum* contains *C. anomalum,* which is native to Asia and is probably not a true pepper since it is nonpungent and has an atypical fruit for the genus. Furthermore, *C. anomalum* lacks certain natural chemical constituents that are present in all other New World peppers and act as predator retardants. The section *Pseudoacnistus* is also monotypic. Its single species, *C. breviflorum,* has the haploid chromosome number of n=13, whereas all true peppers are n=12. This species should probably be removed from *Capsicum.* Within the section *Capsicum, C. ciliatum* also has a chromosome number of n=13 (Pickersgill, 1977), lacks a pungent fruit, and has unusual yellow flowers atypical for the genus. These characteristics suggest that *C. ciliatum* is also not a true *Capsicum.* Other adjustments to a working concept of the genus will undoubtedly have to be made as the various taxa become better known.

The pre-Colombian distribution of the entire genus as defined in this paper is New World. *Capsicum* is a neotropical genus with horizontal range extensions into the subtropics and vertical range extensions into the warm temperate regions of the Andes. The distributions of the domesticated taxa have been detailed by Heiser (1976), Pickersgill (1971) and Eshbaugh (1970, 1979). Heiser (1976) offers a map of the probable pre-Colombian distribution of the domesticated species which provides a working hypothesis which seems reasonable. Nonetheless, the archeological record for peppers is very incomplete. Pepper use can be dated to 7000 B.C. but the species being used is not always certain (Pickersgill, 1969a). Pickersgill (1969b) has traced the archeological record of chili peppers in Peru and indicates the presence of domesticated *C. baccatum* in the coastal region as early as 2500 B.C. Most species of peppers are confined to South America with an especially rich centre of diversity in Brazil. Many species of *Capsicum,* including *C. galapagoensis* (Ecuador) and *C. tovarii* (Peru), are narrow endemics. Perhaps the widest ranging species is *C. annuum* var. *aviculare,* the bird pepper, which occurs from the Amazon to the southern border of the United States, from Arizona to Florida and throughout the Caribbean (D'Arcy & Eshbaugh, 1974).

The domesticated taxa now have a worldwide distribution but at the time Columbus discovered the New World they were much more narrowly distributed. *Capsicum annuum* var. *annuum* was Mesoamerican (Pickersgill, 1971). *Capsicum baccatum* var. *pendulum* was restricted to zones west and east of the Andes (Eshbaugh, 1970; Pickersgill, 1971). *Capsicum pubescens* was a midelevational

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TABLE 1.—A synopsis of the genus _Capsicum_ (Solanaceae) — after Hunziker, 1956, and Eshbaugh, 1980a, with additions and modifications

Strictly wild species		
_C. buforum_*	_C. dusenii_	_C. mirabile_
C. campylopodium	_C. galapagoensis_	_C. parvifolium_
C. chacoense	_C. geminifolium_	_C. scolnikianum_*
var. _tomentosum_*	_C. hookerianum_	_C. schottianum_
C. coccineum	_C. lanceolatum_	var. _flexuosum_*
C. cornutum	_C. leptopodum_	_C. tovarii_*
C. dimorphum	_C. minutiflorum_	_C. villosum_

Domesticated species and spontaneous forms (hypothetical wild ancestors or weedy derivatives)

Domesticated	Wild/Weedy
C. annuum var. _annuum_	var. _aviculare_*
C. baccatum var. _pendulum_*	var. _baccatum_*
	var. _tomentosum_*
	(var.) _praetermissum_*
_C. chinense_*	(?), _C. frutescens_
C. frutescens	_C. frutescens_
C. pubescens	_C. cardenasii_*
	_C. eximium_*
	var. _tomentosum_*

* Taxa added since Hunziker's original treatment.

(2000–2500 m) Andean species (Eshbaugh, 1979). _Capsicum chinense_ and _C. frutescens_ were Amazonian (Pickersgill, 1971).

The domesticated taxa have a unique evolutionary history for seldom have five species been independently domesticated in different geographical regions from one small genus. Early authors recognized and named many supposedly distinct taxa. Other workers chose to lump all the domesticated taxa under a single name _C. frutescens_ (Bailey, 1923) or _C. annuum_ (Shinners, 1956). Investigations of the past 25 years have given us a much clearer understanding of the taxonomy and evolution of the domesticated species. The hypothesis that all the domesticated species arose from a single ancestor (Davenport, 1970; Jett, 1973) is no longer tenable. The opposite hypothesis that each domesticate arose from its own unique wild ancestor seems equally unlikely (Heiser _et al._, 1971). A more likely hypothesis (Eshbaugh, 1980b) which envisages three distinct lines of evolution leading to three subgroups is suggested by data from plant breeding (Emboden, 1961; Eshbaugh, 1964, 1975; Pickersgill, 1971, 1980; Chennaveeraiah & Habib, 1966; Heiser & Smith, 1958; Smith & Heiser, 1957), numerical taxonomy (Pickersgill _et al._, 1979), and isoenzyme analyses (Jensen _et al._, 1979; McLeod, 1977; McLeod _et al._, 1979a, 1979b).

The first of these subgroups, the 'purple flowered taxa,' includes the domesticate _C. pubescens_ and two closely related wild taxa, _C. cardenasii_ and _C. eximium._

The other two subgroups belong to the 'white flowered taxa'. One of these subgroups includes the domesticate _C. baccatum_ var. _pendulum_ and wild _C. baccatum_ var. _baccatum_ and var. _tomentosum_ as well as _C. praetermissum._ Depending upon the treatment, _C. praetermissum_ is seen as a distinct species or variety of _C. baccatum._

The third group includes a complex of three domesticated taxa, _C. annuum_ var. _annuum, C. frutescens,_ and _C. chinense_ and the wild forms of _C. annuum,_ designated var. _aviculare._ The domesticated plants and most of the wild plants are easily classified into distinct species but in some wild plants the distinctions are blurred, perhaps indicating their origin in a single primitive species.

It appears that the domesticated peppers had their centre of origin in south-central Bolivia with subsequent migration and differentiation into the Andes and Amazonia (McLeod _et al._, 1982).

At the time the New World was discovered the only domesticated species to be widespread in the West Indies were _C. annuum_ and _C. frutescens._ Exploration along the east and west coast of South America established contact with _C. chinense_ and _C. baccatum_ var. _pendulum._ Contact with _C. pubescens_ did not come until the explorers reached the Andes. For reasons that remain unclear, the latter two taxa did not become part of the early exchange of plants between the hemispheres. *Capsicum baccatum* var. *pendulum* was introduced to the Old World in the 20th century, whereas *C. pubescens* is still confined to the more mountainous regions of southern Mexico, Central and South America.

The question arises, 'how did *Capsicum* reach the Old World and more particularly Africa?' The most likely explanation suggests several distinct routes for introduction. First, Columbus and other explorers, finding a spice as hot as anything known in Europe, collected this plant and moved it to Europe (Anghiera, 1555). From there the fruits and seeds were probably taken to Africa during the travels of the many explorers of that continent. The earliest introductions were most certainly *C. annuum* and *C. frutescens.* The Spanish and Portuguese were instrumental in the introduction of chilies into western Africa and the Congo Basin (Miracle, 1967). It is also possible that *Capsicum* was introduced as a by-product of trading, missionary work, or colonial invasion.

Second, it is likely that various European botanical gardens were instrumental in introducing *Capsicum* into the colonies of Great Britian, the Netherlands, and France. This remains to be documented. However, it has also been suggested that Arab traders moved *Capsicum* into east Africa. The third, and last important exchange route was by way of the slave trade. It is suggested (Pickering, 1879; McClure, 1982) that ship captains returning to the west coast of Africa introduced many West Indian plants, including perhaps *C. annuum, C. frutescens,* and probably *C. chinense.*

The early history of the introduction of *Capsicum* into Africa is not well documented and is somewhat unclear, but by the 1800's reports of *Capsicum* species began to appear in the literature. Hooker (1849) reported *C. annuum* to be a common cultivated plant in Sierra Leone. Farquhar (1816) listed *C. annuum* and *C. frutescens* in his catalogue of exotic plants cultivated in Mauritius with the comment that *C. frutescens* was naturalized. Jardin (1891) mentioned the presence of wild *C. annuum* var. *aviculare* (= var. *minimum*) in Gabon with the vulgar name Ntogolo. Wherever *Capsicum* was introduced, it became popular as an easily grown cheap spice resource. Today, the market places of most African countries are brightened by quantities of peppers for sale.

Any consideration of pepper production in Africa poses certain difficulties. First and foremost is that reliable statistics are difficult to find and document. Second, peppers are grown for two different uses; first as a green vegetable crop and second as a condiment. In some countries the statistics for these two types of crops are merged while in others they are separate. Table 2 provides some data on area cultivated, yield, and production for green chilies in Africa. The three leading producers of these kinds of peppers are Nigeria, Egypt and Tunisia. However, such statistics fail to show how important red pepper is as a spice in native villages throughout Africa.

This is illustrated in the case of Zaire where production of green chili has been fairly consistent since 1977 at 17 000 metric tons (FAO, 1980). The statistics for 1968 do not indicate that peppers were an important crop at that time (World Atlas of Agriculture). Neither source has anything to say about pepper production as a condiment, yet it is clear (Miracle, 1967) that spice peppers were widely grown in Zaire at this time but primarily for local consumption. He reports that spice peppers have been cultivated throughout Zaire by various tribal peoples including the northern Mongo, a forest dwelling people, who grow the crop intermixed with bananas-plantains, peanuts, tobacco, and various vegetables and that they also have been grown by

TABLE 2.— Chilies + peppers, green production in Africa (adapted from the 1979 FAO Production Yearbook) (5/25/80)

	Area harvested (1000 ha)				Yield (kg/ha)				Production (1000 mt)			
	1969–71	1977	1978	1979	1969–71	1977	1978	1979	1969–71	1977	1978	1979
Africa	124	136	144	148	6649	6953	6858	6980	826	944	989	1032
Egypt	7	8	10	10F	17069	14828	15706	15894	127	123	156	165F
Ghana	28	19	22F	23F	3188	3026	2955	3043	88	59	65F	70F
Ivory Coast	2	3F	3F	3F	8034	7200	7200	7115	16	18F	18F	19F
Libya	1	4F	4F	4F	5373	2250	2250	2250	3	9F	9F	9F
Mauritius					3085	4286	5000	5000	1			
Nigeria	60	65F	67F	68F	8061	9077	8955	9118	484	590F	600F	620F
Sudan			1F	1F	7862	8696	8000	8000	3	4F	4F	4F
Tunisia	23	32F	34F	35F	4013	3906	3529	3657	91	125	120	128
Zaire	3	4F	4F	4F	4010	3951	3952	3953	13	16F	17F	17F

F = FAO estimate.

the northern and southern Songe; the Holohalo; the Lewale; the Banda, who use *C. annuum* as a vegetable and *C. frutescens* as a spice; the Lele, etc.

Another selected example that illustrates the potential for pepper production in Africa is the Malagasy Republic. Pepper production takes place along the south-eastern coast and amounted to 1 900 metric tons in 1965 (World Atlas of Agriculture, 1976). Virtually the entire crop is consumed locally and there is no export market. The crop represents both vegetable and spice peppers. Disease is a serious problem for the crop and may well limit its production. Nonetheless, *Capsicum* production is important and ranks among the top 15 crops for the country.

It is not the intent of this paper to consider production in Africa on a country by country basis. The cases of Zaire and the Malagasy Republic are offered here simply to illustrate several points. First, pepper production is of two types, vegetable and condiment. Second, the reporting statistics do not adequately indicate what kinds of peppers are being grown and for which of the two aforementioned purposes. Third, pepper production is, to a large extent, local and large acreages are seldom given over to growing the crop. Finally, *Capsicum* is rarely an important commercial crop anywhere in Africa.

Today, the most common type of peppers to be found in Africa belong to either the species *C. annuum* (vegetable) or *C. frutescens* (spice). *Capsicum chinense* is present in Africa, but is not nearly so widespread as the other two species which were almost certainly introduced into Africa in the 16th and 17th centuries. *Capsicum annuum* and *C. frutescens* seed is spread by birds. These species have become naturalized in southern Africa and most likely further north.

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Sporoderm morphogenesis in *Euphorbia obesa* and *Croton gratissimus*

M. L. FREAN*

ABSTRACT

Pollen grains of the Euphorbiaceae show a number of pollen types which can be clearly distinguished. Generally different genera are characterized by a specific pollen type. *Euphorbia obesa* Hook. f. and *Croton gratissimus* Burch. subsp. *subgratissimus* (Prain) Burtt Davy, represent two genera within the Crotonoideae with different morphology, each type characteristic for the respective genus.

Taxonomically, the genus *Euphorbia* with apetalous flowers consisting of a naked pistil surrounded by several staminate flowers within a cyathium, is considered more advanced than the genus *Croton.* In *Croton* the inflorescence is a raceme with unisexual flowers. The floral whorls of the male show numerous anthers and both calyx and a showy corolla are present. Both genera are insect pollinated.

In both *Euphorbia obesa* and *Croton gratissimus* the pollen wall in section shows columellae, a structure characteristic of angiosperms. However the present ontogenetic studies show that the formation of the columellae differs entirely in the two pollen types. The final stratification of the wall as well as the morphology of the grains differ and evaluation of the exine structure indicates that phylogenetically *Croton* pollen shows more advanced characters than *Euphorbia* — contradicting the floral phylogeny.

This study conducted at light and electron microscope level compares the two pollen types morphologically and ontogenetically, concentrating mainly on the formation of the exine which is tectate-perforate in the prolate tricolpate grain of *Euphorbia obesa* and semi-tectate in the anaperturate, spheroidal grain of *Croton gratissimus.*

The aim of the study was to evaluate the significance of pollen characters in taxonomic and phylogenetic relationships within the Euphorbiaceae. The differing pollen morphology which is related to the taxonomic grouping of tribes within the subfamily (Crotonoideae) emphasizes diversity, which may result from physiological adaptation. The study shows that the same functional end may well be achieved in different ways and this may be a factor underlying the diversity in the heterogeneous family Euphorbiaceae.

RÉSUMÉ

LA MORPHOLOGIE DU SPORODERME CHEZ EUPHORBIA OBESA *ET* CROTON GRATISSIMUS

Les grains de pollen des Euphorbiacées montrent un nombre de types polliniques qui peuvent être clairement distingués. Généralement, les divers genres sont caractérisés par un type de pollen particulier. Euphorbia obesa *Hook. f. et* Croton gratissimus *Burch. subsp.* subgratissimus *(Prain) Burtt Davy représentent deux genres de Crotonoïdées avec une morphologie différente, chaque type étant caractéristique pour le genre respectif. Taxonomiquement, le genre* Euphorbia *avec ses fleurs apétales constituées d'un pistil nu entouré de plusieurs fleurs staminées dans un cyathium, est considéré comme plus évolvé que le genre* Croton. *Chez* Croton, *l'inflorescence est un racème avec des fleurs unisexuées. Les verticilles de fleurs mâles montrent de nombreuses anthères et tant un calice qu'une corolle bien visible sont présents. Les deux genres sont pollinisés par les insectes.*

Tant chez Euphorbia obesa *que chez* Croton gratissimus, *la paroi du pollen, présente en section des columelles, structure caractéristique des angiospermes. Cependant, les études ontogéniques actuelles montrent que la formation des columelles diffère entièrement dans les deux types de pollen. La stratification finale de la paroi, tout comme la morphologie des grains, diffèrent et l'évaluation de la structure de l'exine indique que phylogénétiquement le pollen de* Croton *motre des caractères plus évolués que celui d'*Euphorbia, *à l'opposé de la phylogénie florale.*

*Cette étude réalisée en microscopie optique et électronique compare la morphologie et l'ontogénie des deux types de pollen, en se basant principalement sur la formation de l'exine, qui est tectée-perforée dans le grain elliptique tricolpé d'*Euphorbia *obesa et semi-tecté dans le grain inaperturé et sphéroidal de* Croton gratissimus. *Le but de cette étude était d'évaluer l'importance des caractères du pollen dans les affinités taxonomiques et phylogénétiques qui existent au sein des Euphorbiacées. La morphologie différente du pollen, qui est en rapport avec le groupement taxonomique des tribus dans la sous-famille des Crotonoïdées souligne la diversité qui peut résulter de l'adaption physiologique. Cette étude montre la même résultat peut bien être atteint de différences manières et ceci peut être un facteur responsable de la diversité dans la famille hétérogène des Euphorbiacées.*

INTRODUCTION

Cronquist (1968) describes the Euphorbiaceae as being highly diverse in anatomy and pollen morphology. *Euphorbia obesa* Hook.f. and *Croton gratissimus* Burch. subsp. *subgratissimus* (Prain) Burtt Davy (referred to as *C. gratissimus* in this study), represent two genera of the heterogeneous family Euphorbiaceae which differ markedly from each other in both their floral structure and pollen morphology while showing morphologically similar pollen within each genus. Both genera are insect pollinated.

Taxonomists generally consider that the trend toward reduction and aggregation culminates in the pseudanthia (or cyathia) of *Euphorbia,* with flowers consisting of a naked pistil surrounded by several staminate flowers (Cronquist, 1968; Stebbins, 1950). In *Croton gratissimus,* the inflorescence consists of a raceme with many male above a few female flowers. The floral whorls of the male consist of numerous stamens bent sharply inwards and both calyx and a showy corolla are present. Taxonomically, the genus

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Euphorbia is considered more advanced than the genus *Croton.* Stebbins (1950) thinks it most probable that the flowers of the Euphorbiaceae became apetalous and unisexual as an adaptation to wind pollination, but have reverted to insect pollination.

Pollen of the Euphorbiaceae has been extensively studied at the light level by Punt (1963) and phylogenetic trends in pollen morphology are noted by Webster (1974). Both *Euphorbia* and *Croton* are genera within the subfamily Crotonoideae* which includes a large number of pollen types. The genus *Euphorbia* has pollen with hippomane-configuration, so-called because the tribes Euphorbiae and Hippomanae in the subfamily Crotonoideae, have almost indistinguishable grains (Punt, 1963). *Croton* is the principal genus among a number of genera of the tribe Crotoneae within the Crotonoideae, which show typical croton-configuration. Morphological differences between the pollen types lie chiefly in the configuration of the mature outer wall, the exine, and in the form and arrangement of the apertures.

Euphorbia obesa and *Croton gratissimus* pollen grains conform to the general pattern for angiosperms (see Heslop-Harrison, 1971). The terminology used is that of Faegri & Iversen (1964). The exine of *Euphorbia obesa* is classically tectate-perforate (Fig. 2a). *Croton gratissimus* (Frean, 1972) has a complex ektexine which may be described as semi-tectate, since it consists of sculptured projections or clavae, partially joined at tectum level (Fig. 2b). Both exine types are columellate. Walker (1976) considers the most likely evolutionary pathway leading to the development of columellae in angiosperm pollen grains is represented by the sequence tectate perforate to semi-tectate. *Croton* with its semi-tectate exine represents a more advanced evolutionary trend.

Therefore, a contradiction is found in *Croton gratissimus* where its floral structure may be less advanced than that of *Euphorbia obesa,* whereas its pollen wall stratification shows more advanced features. This study was undertaken with the aim of establishing the possible taxonomic value and evolutionary significance of sporoderm morphogenesis in *Euphorbia obesa* and *Croton gratissimus.* In this context it shows that the final stratification of the pollen wall is achieved in very different ways in these two entomophilous pollen types. The possible significance of these differences is discussed.

METHOD

Developing and mature anthers of *Euphorbia obesa* and *Croton gratissimus* were examined by light, transmission and scanning electron microscopy to show stages of development of the pollen wall and morphology of the mature grain.

Euphorbia obesa was grown in the greenhouse at the University of the Witwatersrand, Johannesburg. *Croton gratissimus* was collected from the Daspoort range near Pretoria. Voucher specimens of these two species are lodged with the Moss Herbarium (J), Johannesburg. Other *Euphorbia* and *Croton* spp. were examined by light and scanning electron microscopy to provide confirmation of the generic pollen type. Pollen of *Croton dideroides* M. Denis, *Euphorbia esculenta* Marl., *E. ferox* Marl., *E. gariepina* Boiss., *E. meloformis* Ait. and *E. splendens* Boj. ex Hook. var. was obtained from the hothouse, Botanical Research Institute, Pretoria; pollen of *Croton zambesicus* Muell. and *C. sylvaticus* Hochst. was taken from specimens in the Moss Herbarium.

Euphorbia obesa

Plants are dioecious, producing 5 rows of bilobed anthers in a cyathium. The anthers mature in ascending order in each row, so that a single cyathium shows anthers and pollen at many stages of development.

Croton gratissimus

Plants are monoecious. The inflorescence consists of a raceme with many male flowers above a few female ones. Anthers are arranged in whorls, the youngest being in the inner-most whorl. Anthers of both species were processed routinely for light, transmission and scanning electron microscopy. The methods used have been previously described by Frean (1972).

Light microscopy

Fresh anthers were squashed in Belling's aceto-carmine (Gatenby & Beams, 1950).

For sectioning, entire cyathia of *Euphorbia obesa* and buds of *Croton gratissimus,* stripped of bracts, were fixed in formalinacetic-alcohol, dehydrated in ethanol and tertiary-butyl-alcohol (Johansen, 1940), embedded in wax and sectioned at 5–8 μm. Longitudinal sections mounted serially on slides, provided a wide range of developmental stages. This material was stained with the periodic acid — Schiff (PAS) reaction for polysaccharides (Humason, 1967) to show cellulosic primexine and intine.

Transmission electron microscopy (TEM)

Anthers were fixed at 4°C in 2% glutaraldehyde in 0,1 M cacodylate buffer at pH 7,3 for 1 hour, postfixed in 1% osmium tetroxide in the same buffer for 1 hour, dehydrated in a graded acetone series and embedded in Luft's (1961) epon.

Sections, cut at 60–90 μm, were picked up on 200 mesh copper grids and stained with a saturated solution of uranyl acetate in 50% alcohol for 10 minutes, followed by 2 minutes in Reynolds's (1963) lead citrate. They were viewed at 80 KeV in a Jeol JEM 1000 conventional TEM.

Scanning electron microscopy

Mature anthers were processed in a Polaron Critical Point Apparatus E 3800, after routine fixation for transmission electron microscopy. Anthers from herbarium specimens were dissected from *Croton* buds prior to fixation. Critical point

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* Editor's note: Crotonoideae = Euphorbioideae.

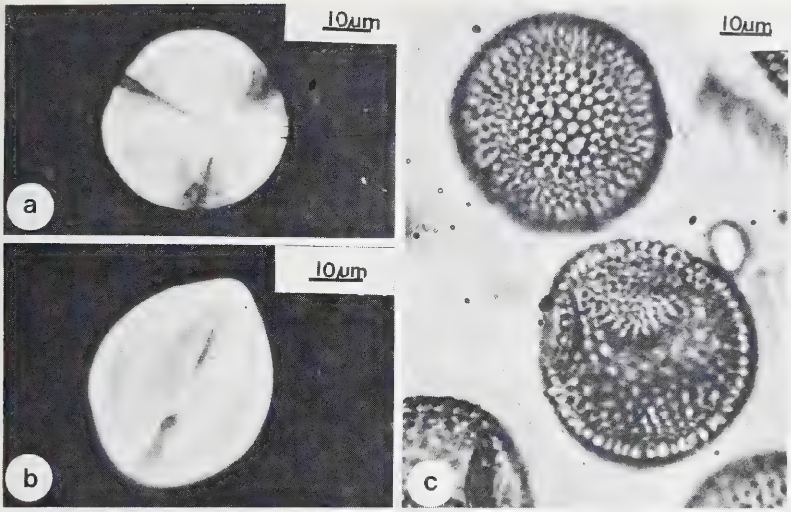

FIG. 1.—Acetolysed grains. a, *Euphorbia obesa,* polar view. b, *E. obesa,* equatorial view. c, *Croton gratissimus.*

dried anthers were broken open onto stubs lightly coated with colloidal graphite, then coated with gold palladium and viewed in an S_4 Cambridge stereo-Scan-EM.

Acetolysis

Resin-embedded sections of material routinely embedded for transmission electron microscopy and mounted on glass slides, were acetolysed on a microscale (Dickinson & Bell, 1972) with a 9:1 acetic anhydride/sulphuric acid mixture. By this technique, combined with the PAS reaction, the stage at which protosporollenin became polymerized to sporopollenin was established.

RESULTS

Light microscopy

Acetolysed grains show that at light microscope level, *Euphorbia obesa* conforms to the hippomane configuration, except that it is without a true pore. The grain is tricolpate rather than tricolporate (Fig. 1a, b).

Croton gratissimus shows typical croton-configuration, appearing tectate with clavae rising above the tectum (Fig. 1c), but electron microscopy shows that grains are semi-tectate rather than tectate. Grains are spherical and anaperturate.

Transmission electron microscopy

Final wall stratification in grains of *Euphorbia obesa* and *Croton gratissimus* is shown diagrammatically in Fig. 2a, b. The following stages (1–4) are described:

1. *Early exine formation*

In both species the first sign of activity at the plasma membrane, related to wall formation, occurs at the late pachytene stage of meiosis in the callose enclosed microspore mother cell (Fig. 3a, b). A matrix layer appears outside the plasma membrane, closely associated with distended ends of rough endoplasmic reticulum in the cytoplasm. This layer is possibly mucopolysaccharide in nature. Within this layer the PAS-positive, cellulosic primexine is laid down, serving as a template within which the ektexine elements form.

2. *Growth of the exine elements*

In *Euphorbia obesa* further development of the ektexine takes place at the tetrad stage. At the surface of the primexine, flask-shaped vesicles appear (Figs 3c & 4c). They appear to move out with the primexine as it forms. These vesicles are so arranged that by excluding both the formation of the primexine fibrils and the laying down of the ektexine in these regions, they form the perforations of the tectum.

Concomitantly with the formation of the vesicles and the primexine, columellae form on specialized areas of the plasma membrane (Fig. 4a, c). By the end of the tetrad stage the bases of the columellae are joined by the foot-layer (Fig. 4c). The ektexine now is PAS-positive, but not acetolysis resistant, and resembles the early matrix material in texture (?mucopolysaccharide). It is composed of protosporopollenin with some final polymerisation evident

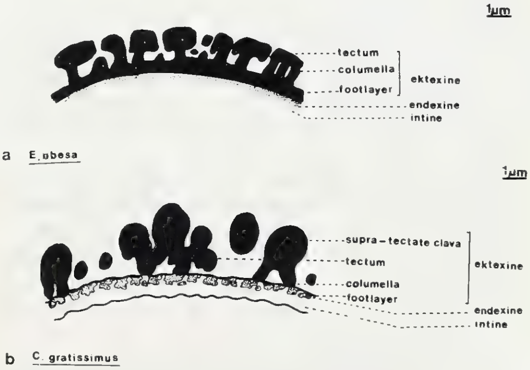

FIG. 2.—Diagrammatic representation of the mature pollen wall as seen in section by transmission electron microscopy. a, *Euphorbia obesa.* b, *Croton gratissimus.*

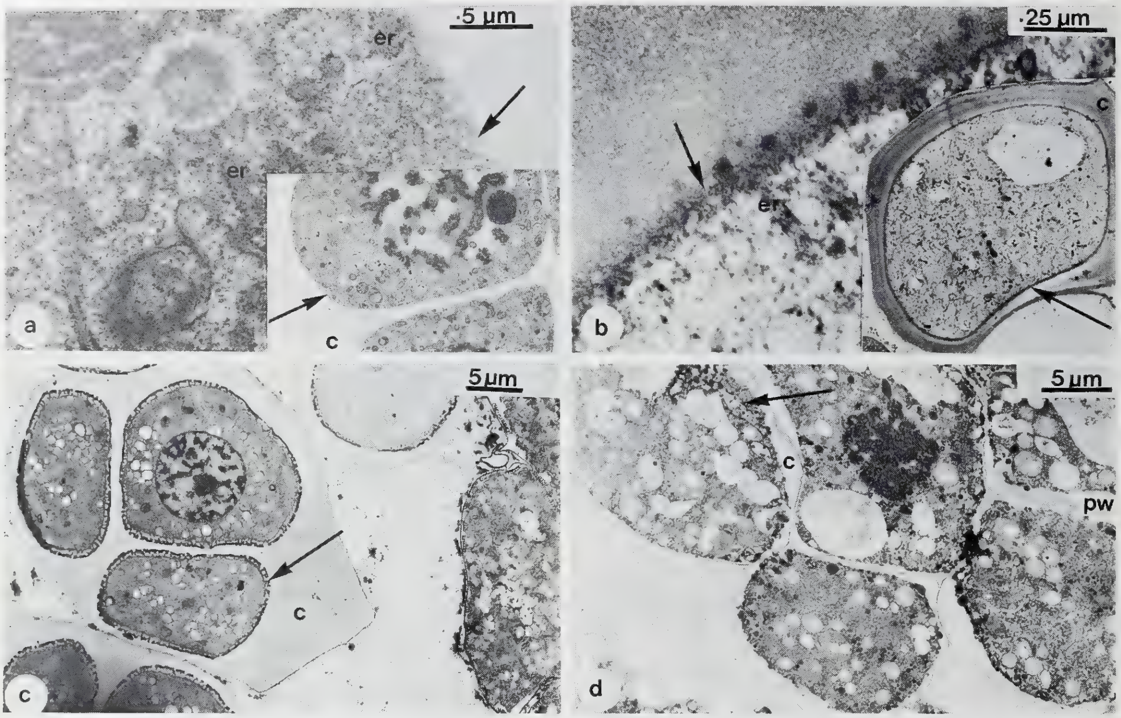

FIG. 3.—Early wall formation. a, *Euphorbia obesa,* matrix material is seen at the plasma membrane (arrowed). *Inset:* microspore mother cell, pachytene stage, wavy plasma membrane (arrowed) is characteristic of early wall formation; c = callose. b, *Croton gratissimus,* matrix material (arrowed) is seen at plasma membrane with early ektexine elements. *Inset:* microspore mother-cell, early signs of wall formation are visible (arrowed); c = callose. Note that in both grains elements of the endoplasmic reticulum (er) with distended cisternae are associated with early events outside the plasma membrane. c, *E. obesa,* callose-surrounded tetrad, ektexine elements arrowed; c = callose. d, *C. gratissimus,* late stage of microspore mother cell, ektexine elements arrowed; c = callose, pw = primary wall.

in the osmiophilic (lipoidal) regions of the ektexine (Fig. 4c).

At this time the apertural regions of the microspore are defined. In the central colpus area (there is no true pore) a plug of matrixlike material is formed (Fig. 5c).

In *Croton gratissimus* development of the ektexine takes place largely during the microspore mother cell stage. (Fig. 3d). Globular outgrowths seen in stage 1 (Fig. 3b) enlarge. They appear to consist of lipid surrounded by ribosome-like particles. These structures, the future clavae, enlarge, but smaller globules continue to form outside the plasma membrane (Fig. 4b, d). They are not strongly PAS-positive and show early acetolysis resistance, suggesting a different composition with more lipid in the early stages, than in *Euphorbia obesa.*

The layers of the ektexine, tectum, columellae and footlayer, now complete, are finally polymerised in the thecal fluid on release from the callose wall in both grains. In this they are typical of many angiosperm grains.

3. *Endexine formation*

In both grains electron lucent lamellae of unit membrane core dimensions, on which osmiophilic material (?sporopollenin) accumulates, separate endexine and ektexine. In *Euphorbia obesa* the osmiophilic material forms an endexine element outside the plasma membrane. Movement of this element through an apparent space separating ekt- and endexine, results in its apposition to the lower surface of the foot-layer. Here a number of elements are applied, become compacted and form a homogeneous layer. Evidence that they are membrane derived, remains in the form of lucent cores (Fig. 4e) or 'white lines' (4–5 nm). During this period the apertural plug is transformed into the lamellate structure of the mature aperture (Fig. 5d) by the invasion of protoplasmic tubules.

In *Croton gratissimus* ribosome-coated globules fill the endexine space (Fig. 4f). These globules polymerise to form electron dense bodies in an inter-bedded zone which consists of endexine and intine (Fig. 5e). The derivation of the electron lucent lamellae or 'white lines' was not traced in this grain.

4. *Intine formation*

Presence of the intine layer is confirmed by the PAS-reaction confirming its cellulosic nature. A special feature of the intine in *Euphorbia obesa* lies in the formation of intine reservoirs on each side of the central aperture (see inset, Fig. 5a). In *Croton gratissimus* two layers can be distinguished in the intine — an inner layer with cytoplasmic inclusions in the fibrillar ground substance and an outer layer forming the inter-bedded zone. Vesicles, apparently

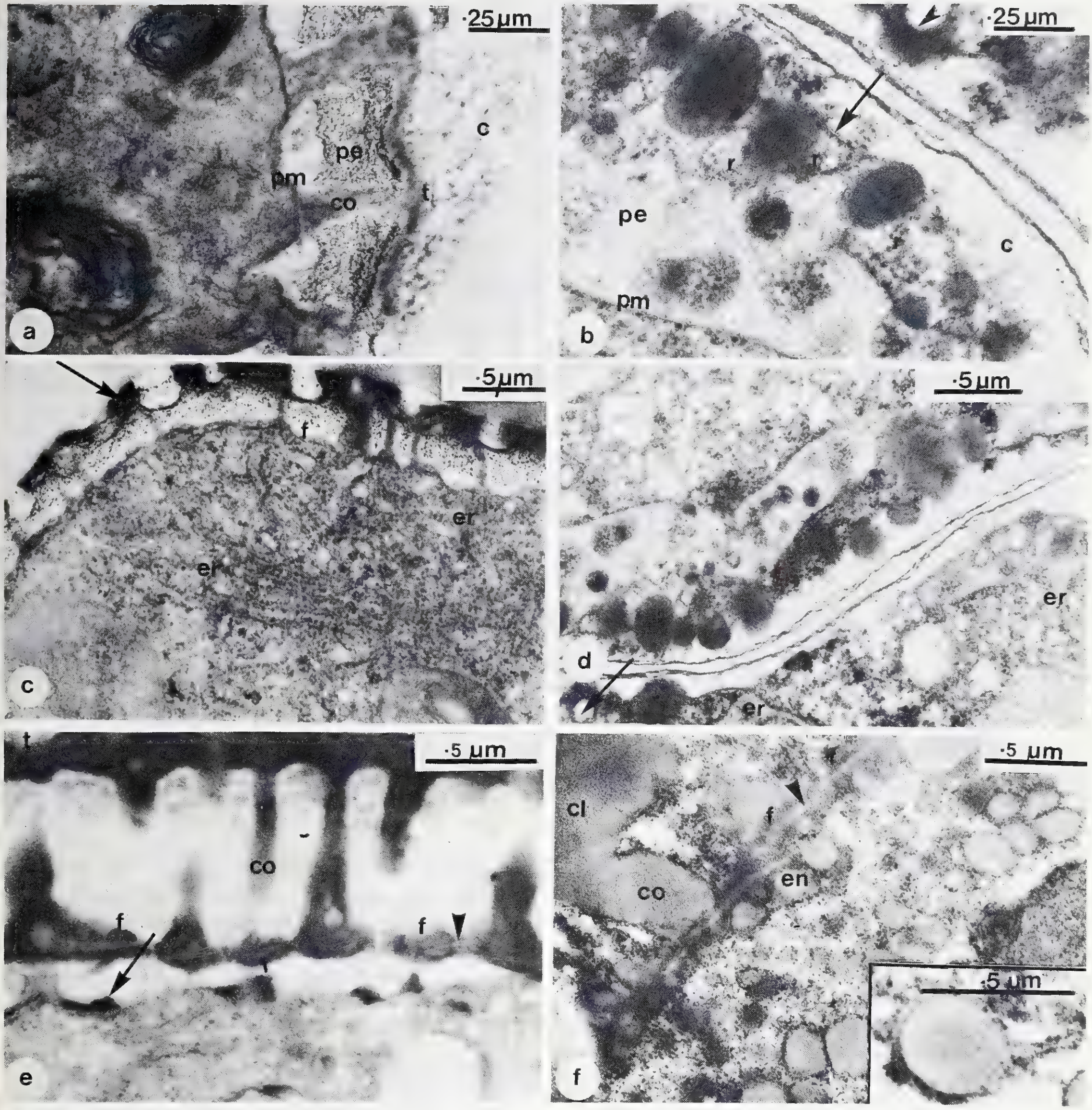

FIG. 4.— Growth of ektexine elements. a, *Euphorbia obesa,* ektexine elements viz columellae (co) and tectum (t) showing finely textured appearance; c = callose, pe = primexine, pm = plasma membrane. b, *Croton gratissimus,* globular outgrowths (clavae) some with lucent cores (arrowhead) appear to be ribosome surrounded (r) and show intimate association with membranes of unit membrane dimensions (arrowed), cf with plasma membrane (pm) at the cytoplasm surface; c = callose, pe = primexine, pm = plasma membrane. c, *E. obesa,* microspore cytoplasm with ektexine. Note arrays of tubular, rough endoplasmic reticulum (er), polymerizing osmiophilic regions of the tectum (arrowed), and formation of the footlayer (f). d, *C. gratissimus,* microspore cytoplasm with ektexine. Note tubular ribosome coated endoplasmic reticulum (er) associated with the plasma membrane, and electron lucent cores of clavae (arrowed, lower left corner). e, ektexine polymerization and endexine formation. *E. obesa,* ektexine showing evidence of polymerization in enhanced osmiophilia. Note that some areas remain unpolymerized (less electron dense), at the plasma membrane an endexine element (arrowed) is forming, while a second element above it is being applied to the footlayer (f) of the ektexine, white lines are visible in the endexine (arrowhead); co = columella, t = tectum. f, *C. gratissimus,* growth and polymerization. Note columella (co), footlayer (f) and globular elements of the endexine (en). *Inset:* small ektexine globule.

empty, appear in the inter-bedded zone and among the ektexine elements as final wall stratification is achieved. These resemble 'fusiform vesicles' as described by Rowley & Erdtman (1967) in *Populus* and represent the remains of cytoplasmic membranes.

Scanning electron microscopy

Fig. 6 shows the surface morphology of mature grains of *Euphorbia obesa* with a tectum perforatum and *Croton gratissimus* with clavae at supra-tectal level.

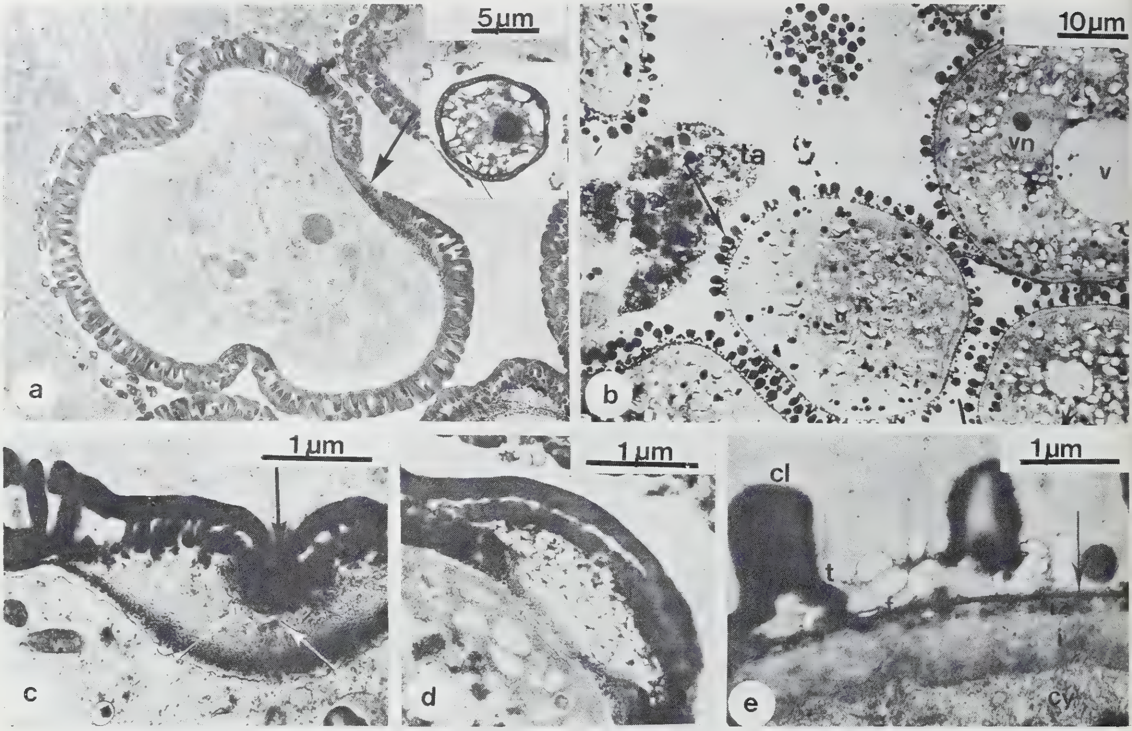

FIG. 5.—Final exine stratification and intine formation. a, *Euphorbia obesa,* apertures arrowed, inset shows mature grain with intine reservoirs (arrowed). b, *Croton gratissimus,* tectate areas arrowed, clavae rise above tectum. c, *E. obesa,* fibrillar material of aperture shows apertural exine (black arrow) and invasion of fibrillar plug by protoplasmic tubulus (white arrows). d, *E. obesa,* final lamellate appearance of aperture. e, *C. gratissimus,* final appearance of the pollen wall; cl = clavae, f = footlayer, t = tectum, i = intine, iz = interbedded zone, fusiform vesicles arrowed, cy = cytoplasm.

DISCUSSION

This investigation shows that *Euphorbia obesa* and *Croton gratissimus* differ morphologically in the stratification of the sporoderm and morphogenetically in its formation. Both grains are columellate, a feature considered to be characteristic of angiosperms (Walker, 1976). However, achievement of columella formation differs markedly in these two taxonomically related genera.

1. *Ontogeny*

(a) *Formation of the columellae (ektexine)*

In *Euphorbia obesa* the plasma membrane appears to influence exine form in providing recognition sites at which the columellae form (Fig. 4a). Such definitely defined sites were not seen in *Croton gratissimus,* and plasma membrane involvement is not as clearly delimited.

In contrast, involvement of membranes in ektexine formation is dramatically evident outside the plasma membrane during ektexine formation in *C. gratissimus.* Although their actual derivation from the plasma membrane or the cytoplasm is obscure, their dimensions (10 µm in width) conform to those of the plasma membrane (Fig. 4b). These membranes are associated with globular elements of the ektexine, and with ribosomelike particles. The unusual occurrence of ribsomelike particles on the exine-forming side of the plasma membrane is outside the scope of this discussion. The globular elements increase in size during this stage.

Lamellae of unit membrane dimensions have been described in exine formation in other grains, e.g. in *Lilium* (Dickinson & Heslop-Harrison, 1968). However, the situation in *Croton gratissimus* where a system of growth by apposition of material from the inside is suggested (see also *Polyceratocarpus* in the Annonaceae, Le Thomas & Lugardon, 1976) is very different from the precisely controlled development of a typical columellar exine as seen in *Euphorbia obesa* or *Lilium,* which in turn differ from each other in the precise mechanism of columella formation.

The characteristic pattern of the pollen wall in flowering plants is established by the maternal cytoplasm of the pollen mother cell (Rogers & Harris, 1969; Heslop-Harrison, 1971). The mechanism by which the cytoplasm forms the pattern is not clear. However, it does seem clear, even from the limited number of pollen types dealt with in this discussion, that although columellae are characteristic of angiosperm pollen and are considered to serve a common purpose in providing structure which increases exine flexibility and houses sporophytic proteins (Muller, 1979; Heslop-Harrison, 1971), they differ in construction and ontogeny.

(b) *Endexine formation*

Although the final appearance of the endexine differs greatly in *Euphorbia obesa* and *Croton*

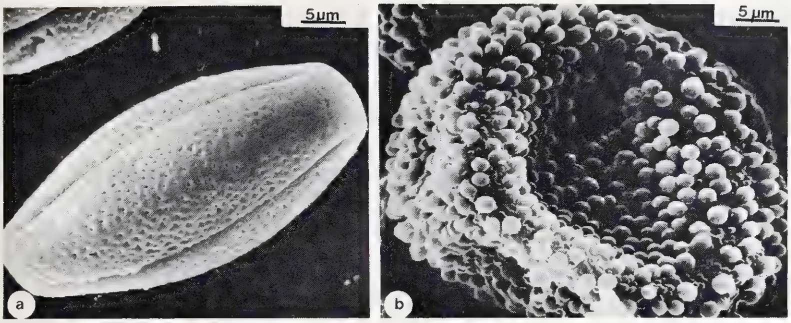

FIG. 6.—Scanning electron micrographs. a, *Euphorbia obesa*, b, *Croton gratissimus*.

gratissimus (Fig. 5e, f), membrane involvement remains evident in the form of 'white lines' of unit membrane core dimensions. Formation of the endexine appears to follow an established angiosperm pattern as described in many grains e.g. *Lilium* (Dickinson, 1976). The term 'white lines' is used by Godwin, Echlin & Chapman (1967) in their description of endexine formation in *Ipomoea.*

In *Croton gratissimus* the interbedded endexine appears to afford the grain a capacity for expansion provided by the lamellate apertures in *Euphorbia obesa.*

The ubiquitous mode of formation of the endexine (when present) in angiosperms is consistent with the rôle of a layer perhaps more limited in function than the ektexine where adaptation to environmental influences such as dehydration, compatibility, pollen vectors, may influence more strongly the evolution of characteristic exine patterns.

(c) *Intine formation*

In *Euphorbia obesa* the intine reservoirs may provide extra sites to house enzymes (Knox & Heslop-Harrison, 1970) since this layer in other parts of the grain is extremely thin. They also have a harmomegathic function in accommodating grain expansion.

In *Croton gratissimus* the thick intine may provide additional enzyme sites, compensating for the rather open, semi-tectate ektexine.

In concluding this section of the discussion it can be stated that in many ways these two pollen types appear to be achieving the same end point despite wide differences in pollen ontogeny and morphology.

2. *Morpho-physiological adaptation*

A further comparison which can be made between these two grains is their response to hydration. Both show a great capacity for expansion. In *Euphorbia obesa* the accommodation mechanism for expansion of this tricolpate grain lies in the granular endexinous apertural floor, apertural lamellations and in the position occupied by two intinous reservoirs, one on each side of the presumptive pore; there is no true pore. *Croton gratissimus* in common with many Crotoneae, has large spherical pollen grains (±50 µm in diameter), is aporate and has a semi-tectate exine with massive supra-tectal projections. Breckon & Webster (1974) show that when the grain is turgid the tectal pegs spread apart exposing the layers below while dehydration results in shrinkage pulling the tectal pegs together, with their apices forming a continuous ektexine which may contribute to the elasticity of the exine in these aporate *Croton*-type grains. The thin inter-bedded endexine may contribute to this elasticity.

Whatever the cause of these adaptive modifications of the sporoderm morphology to changes in physiological conditions, the resulting features must underlie some of the taxonomic heterogeneity of this family. In relating morphological wall features to current taxonomic and phylogenetic concepts, it is noted that the number of species examined is small. However, the members of the genus *Euphorbia* and of the genus *Croton* which are compared, are

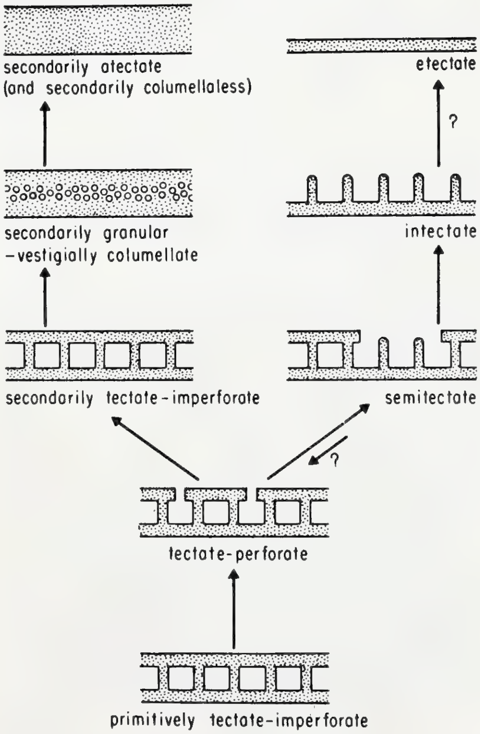

FIG. 7.—Diagram of evolutionary trends within the angiosperms (Walker, 1976).

representative of their morphological types or 'configurations' as described by Punt (1963).

3. *Evolutionary status of the pollen wall*

The exine of *Euphorbia obesa* is classically tectate-perforate (Figs 2a, 5a & 6a). *Croton gratissimus* has a complex ektexine which may be described as semi-tectate, since it consists of sculptured projections or clavae partially joined at tectum level (Figs 2b, 5b & 6b). Both exine types are columellate. Walker (1976) considers that the most likely evolutionary pathway leading to the development of columellae in angiosperm pollen grains is represented (as shown in Fig. 7) by the sequence tectate-perforate to semi-tectate. *Croton* with its semi-tectate exine would thus represent a more advanced evolutionary trend.

Walker suggests that although there is no strong correlative evidence to suggest that pollen which has already reached the semi-tectate stage can reverse back to tectate-perforate, future studies may indicate that such a reversal can occur. Within the boundaries of present concepts this study shows that a contradiction is found in *Croton gratissimus* where its floral structure may be less advanced than that of *E. obesa,* whereas its pollen wall stratification may show more advanced features.

FINAL REMARKS

This study achieves its main stated aim, namely that of examining and describing ontogeny and morphological stratification of the sporoderm in *Euphorbia obesa,* and *Croton gratissimus* subsp. *subgratissimus,* and indicates the importance of ontogenetic studies in interpreting the final structure of the pollen wall.

The diversity of pollen walls reflects adaptive function. As this study shows, pollen walls not only reflect the possible selective pressures to which the various functions of the grain have been exposed in the course of evolution, but shows that the same functional end may well be achieved by different means (Heslop-Harrison, 1979).

The differing morphology of the two pollen types emphasizes diversity within a family which may result from physiological adaptation, and highlights some taxonomic and phylogenetic problems in the family Euphorbiaceae, with its diverse floral structure and pollen morphology.

There is no comprehensive theory according to Cronquist (1968):

> 'of how selection could drive the inflorescence through a full cycle from normal flowers to separate reduced unisexual flowers and then to pseudanthia (or cyathia) in *Euphorbia,* although it seems logical to suppose that the organisation of the inconspicuous reduced flowers of *Euphorbia* into a cyathium represents a return to ordinary entomophily'.

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Evolution of succulent *Euphorbia* as interpreted from latex composition

P. G. MAHLBERG*, J. PLESZCZYNSKA*, W. RAUH** and E. SCHNEPF**

ABSTRACT

The morphology of starch grains and the gas-liquid chromatographic profile of triterpenes derived from latex of the nonarticulated laticifer of succulent African *Euphorbia* were examined for their applicability to interpret phylogenetic relationships of this genus. Several trends in starch grain morphology and triterpene composition were evident in the 38 examined taxa. Rod shaped grains, interpreted to be conservative, occurred in only a few taxa in several dwarf groups. Grains of osteoid shape prevailed in most taxa. Highly osteoid grains possessing lobed ends represented the most complex form and were present in some taxa endemic to Madagascar. Triterpene profiles which contained from 2 to 14 or more compounds were derived from all taxa. Each taxon possessed a characteristic profile, or identifying fingerprint. The composition of the profile differed quantitatively and qualitatively among taxa. Taxa with few triterpenes, tentatively interpreted as primitive, occurred in dwarf forms, whereas Madagascan taxa tended to possess high numbers of triterpenes reflective of specialization. This study supports the interpretation that laticifer starch grain morphology and triterpene composition, both gene mediated stable markers, can be employed to determine and correlate phylogenetic relationships between taxa of this complex genus.

RÉSUMÉ

L'ÉVOLUTION DES EUPHORBES SUCCULENTES INTERPRÉTÉE À DE LA COMPOSITION DU LATEX

*La morphologie des grains d'amidon et le profil chromatographique gaz liquide de triterpènes du latex des laticifères non articulés d'*Euphorbia *succulents africains ont été examinés pour leur possibilé d'application dans l'interprétation des relations phylogénétiques de ce genre. Plusieurs tendances dans la morphologie du grain d'amidon et la composition du triterpène furent évidentes dans les 38 taxa examinés. Des grains en forme de bâtonnets, interprétés comme primitifs furent observés dans quelques taxa seulement de plusieurs groupes nains. Des grains à forme ostéoïde prédominèrent dans la plupart des taxa. Des grains fortement ostéoïdes possédant des bouts lobés représentèrent la forme la plus complexe et furent présents chez certains taxa endémiques de Madagascar. Les profils de triterpènes qui contenaient de 2 à 14 composés ou plus furent obtenus de tous les taxa. Chaque taxon possédait un profil caractéristique, ou empreinte digitale d'identification. La composition du profil différait quantitativement et qualitativement parmi les taxa. Les taxa avec peu de triterpènes, interprétés provisoirement comme primitifs, se rencontraient dans les formes naines, tandis que les taxa malgaches avuient tendance à posséder des nombres élevés de triterpènes tradvisant une spécialisation. Cette étude prouve que la morphologie du grain d'amidon du laticifère et la composition du triterpène, toutes deux indicatrices stables des gènes, peuvent être employés pour déterminer et mettre en corrélation les relations phylogénétiques entre les taxa de ce genre complexe.*

INTRODUCTION

The genus *Euphorbia* is characterized by the presence of the nonarticulated laticifer which contains specialized components in its protoplasm, or latex, that can be utilized to interpret the evolution of this cell type as well as taxonomic relationships within the genus. Previous studies have shown that starch grains within laticifer plastids possessed a characteristic morphology for a taxon and morphological groups within this genus (Mahlberg, 1973, 1975; Biesboer & Mahlberg, 1981). Several investigations also have indicated that the triterpene profile and composition of latex differed for groups of taxa (Ponsinet & Ourisson, 1965, 1968; Anton, 1974; Biesboer, 1979). In a recent study it was emphasized that a taxon including cultivars possessed a characteristic triterpene profile which was genetically stable under diverse conditions (Biesboer, 1979; Biesboer, D'Amour, Wilson & Mahlberg, 1982).

Mahlberg (1975) emphasized the potential importance of utilizing the laticifer and its various components to interpret phylogeny at the species level. Laticifers in *Euphorbia* synthesize and accumulate many specialized products such as modified starch grains and triterpenes which appear to represent useful markers for such studies.

The succulent *Euphorbia* of Africa and adjacent islands represent a large assemblage of taxa of diverse habit. Their evolution remains as yet unclear, although they appear more highly specialized than nonsucculent leafy forms of this genus. Webster (1967) suggested that the subgenus *Euphorbia* may have originated from the subgenus *Esula*, whereas Kuzmanov (1964) maintained that woody forms of subgenus *Esula* were derived from primitive forms of the subgenus *Euphorbia*. The succulent forms have been classified primarily on morphological features associated with their habit (Berger, 1907; White, Dyer & Sloane, 1941; Jacobsen, 1954) since it has been difficult to utilize floral characters to distinguish between species. Yet in Jacobsen's book, which combines the works of Berger as well as White, Dyer, and Sloane, there are taxa of different habit included within most of the 27

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different groups of succulent *Euphorbia* recognized by him.

The purpose of this study is to examine whether the laticifer markers, both starch grain morphology and triterpene profile, can be utilized to distinguish between taxa of succulent *Euphorbia* and provide insight into their phylogeny. Representative taxa of nearly all groups from Jacobsen (1954) are examined for these two character markers.

MATERIALS AND METHODS

Latex was collected from succulent plants at the Botanical Garden of the University of Heidelberg. The shoot was scarified within several centimetres of the apex, and the latex exudate was collected both onto microscope slides for examination of starch grains and into vials containing acetone (analytical grade) for extraction of triterpene components.

For starch analysis, drops of exuded latex on microscope slides were stained with one drop of aq IKI, spread uniformly over the slide surface, air dried at least 24 hr, and mounted in resin for a permanent record. Three slides were prepared from more than one specimen when available in the succulent collection. Fifteen mature starch grains (those of large size) on each slide were recorded for shape and measured for length and width at the midregion as well as end of the grain. Tabulated information represent calculations from at least one slide of a specimen and standard deviations were determined for these data (Mahlberg, 1975).

For gas-liquid chromatography the acetone supernatant containing triterpenes was filtered into a fresh vial and evaporated to dryness over nitrogen. The residue was resuspended in 1 ml spectranalysed grade acetone to make a stock solution. One or 3 μl quantities of stock were transferred into fresh tubes and evaporated over nitrogen to dryness. These residues were resuspended in 0,5 ml spectranalysed grade acetone containing 0,5 mg/ml Δ^4-androsten-3,17-dione (androstendione) as an internal standard. One μl of each sample was injected onto the chromatographic column. Analyses were performed on a Hewlett-Packard 5710A gas-liquid chromatograph equipped with a flame ionization detector and operated by programming from 240−310 C at 4°/minute. Nitrogen was used as the carrier gas (20 ml/min flow rate). The injection port temperature was 250°C; the detector temperature was 300 or 350°C. Glass columns (2 mm ID × 2,43 m) were treated with 5% dimethyldichlorosilane in toluene and packed with 3% OV−1 on 100/120 mesh Supelcoport. Individual compounds were quantified on a Hewlett-Packard 3380A integrator with data on detected peaks expressed as area percent.

Specific compounds were identified from known and mass spectral analyses of extracts from particular species (Biesboer *et al.*, 1981; Mahlberg, unpublished) and from the identified retention times for several hydrocarbon compounds employed as external standards, including β−amyrin, campesterol, cycloartenol, ergosterol, euphol, germanicol, sitosterol, stigmasterol, and tirucallol.

The coinjection technique utilizing external standards also was employed to identify compounds for a taxon.

Sources of materials. Living specimens in the Botanical Garden at the University of Heidelberg were represented by: *E. acrurensis* N.E. Br; *E. aggregata* Bgr. 8995; *E. albertensis* N.E. Br. 31936; *E. balsamifera* Ait. 41180; *E. bubalina* Boiss. 9505; *E. capuronii* U. & L. M1790; *E. clavarioides* Boiss. 47015; *E. davyi* N. E. Br. 46753; *E. decaryi* Guill. 21984; *E. delphinensis* U. & L.; *E. didiereoides* Denis M1534; *E. echinus* Hook. f. & Coss. 41179; *E. ecklonii* Hassl. 46767; *E. fasciculata* Thunb. 33505; *E. fiherenensis* Poiss. 11957; *E. francoisi* Leandri 22105; *E. globosa Sims* 5281; *E. groenewaldii* Dyer 39417; *E. hamata* Sweet 3590; *E. maleolens* Phill. 3011; *E. melanohydrata* Nel 32131; *E. neohumberti* Boit. 9086; *E. nyikae* Pax 23284; *E. obesa* Hook. f. 7599; *E. pentagona* Haw. 17397; *E. persistens* Dyer 47115; *E. piscatoria* Ait. 32423; *E. pseudotuberosa* Pax 33506; *E. sudanica* Chev. 19948; *E. susannae* Marl. 45790; *E. trapaeifolia* Chev. 19623; *E. trichadenia* Pax 46995; *E. unispina* N.E. Br. 4643; *E. valida* N.E. Br. 4926; *E. woodii* N.E. Br. 8708; and *E. xylophylloides* Brongn. 8948. Specimens grown at Indiana University included *E. tirucalli* L. 102 and *E. viguieri* Denis 47.

RESULTS

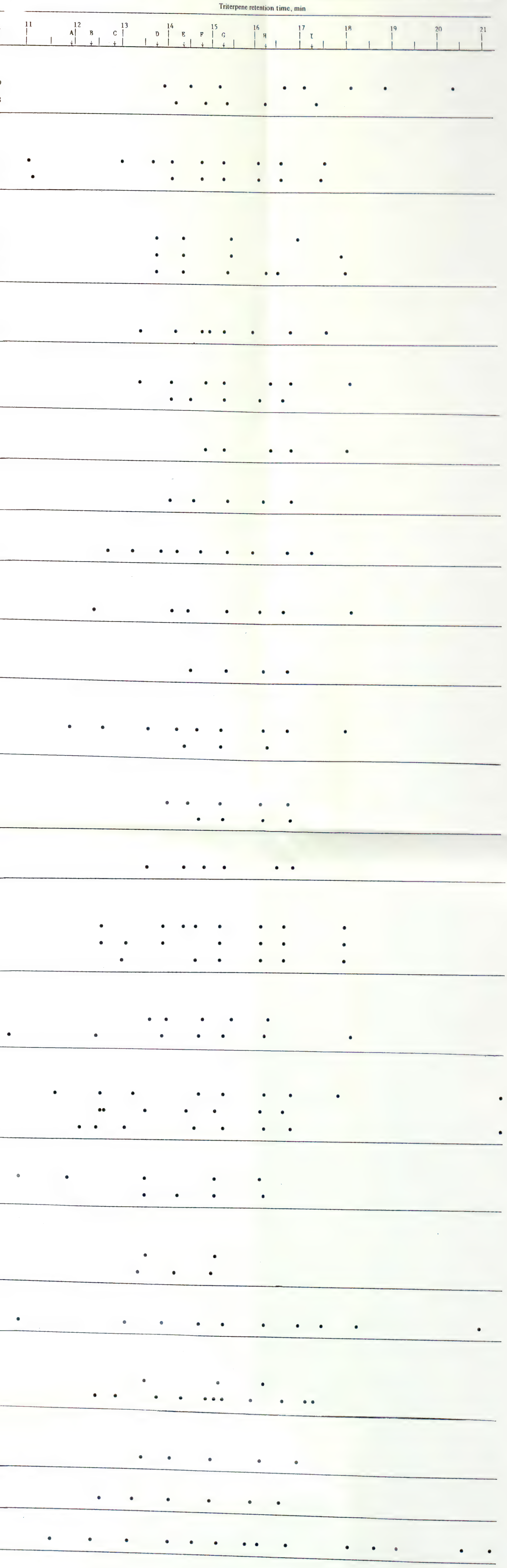
All taxa examined in this study yielded copious quantities of latex from laticifers for these analyses. The latex color was typically white, although in some species it was tinted yellow. Latex protoplasm is derived from the nonarticulated laticifer which is distributed throughout most tissues of the axis in *Euphorbia*.

Starch grains were abundant in exudate derived from the 38 taxa examined in this study. Comparison of their morphological form showed that most taxa possessed osteoid-shaped starch grains as the mature grain form, whereas others possessed rod-shaped grains (Table 1). The rod type or the modified spindle form were present in only a few taxa such as *E. trichadenia* Pax (group 7) and *E. ecklonii* Hässl. (group 8). The degree of osteoidy can be recognized upon comparison of the width at the midregion and end of the grain. The ends of grains of taxa in several groups as 6, 8, 9, 18, are only slightly larger than the midregion and appear somewhat osteoid in form. For other taxa the end of the grain is considerably enlarged as in groups 4, 15, 17, 19, 22, and may measure greater than twice the width of the midregion as in groups 1, 2, 12, 20, and the Madagascan groups.

Starch grain length, expressed as an average size for the larger grains present in the sample, differed among examined taxa (Table 1). Their length ranged from short grains, 21,6±3,4 μm in *E. unispina* N.E. Br. (group 25), to very long grains, 46,6±9,9 μm in *E. ecklonii.* The short starch grains as in *E. unispina* (21,6 μm) and *E. delphinensis* U. & L. (22,3±3,2 μm, group 20) represented a distinct size class which differed significantly from larger grains in latex of

TABLE 1.—Starch grain and triterpene (sterol) characters of *Euphorbia* taxa, classified according to Jacobsen (1954)

Group/taxon	Starch grain Shape	Length µm	Width, µm Mid	Width, µm End
Group 1. Bushes, cylindrical leafy branches; 11 taxa				
E. balsamifera Ait.	Osteoid(b)	36.5±3.6	7.5	17.9
E. piscatoria Ait.	Osteoid	32.5±3.5	6.6	8.8
Group 2. Shrubs; branches thickened near apex; leafy; 7 taxa				
E. neohumberti Boit.	Osteoid	33.0±4.0	5.1	12.1
E. viguieri Denis	Osteoid	31.0±2.7	6.0	8.8
Group 4. Coralline shrubs; leaves soon falling; 62 taxa				
E. fiherenensis Poiss.	Osteoid	30.4±4.9	5.2	9.6
E. tirucalli L.	Osteoid	44.6±2.4	7.8	13.8
E. xylophylloides Brongn.	Osteoid	34.0±8.5	7.0	10.4
Group 6. Shrubs; tuberculate branches; leaves soon falling; 5 taxa				
E. hamata Sweet	Osteoid	36.3±6.4	6.2	8.0
Group 7. Dwarf; leafy branches from caudex; 4 taxa				
E. pseudotuberosa Pax	Osteoid	33.6±6.4	5.4	7.5
E. trichadenia Pax	Rod	31.7±2.2	4.7	4.7
Group 8. Dwarf; short leafy stem; 6 taxa				
E. ecklonii Hassl.	Rod	46.6±9.9	6.6	7.7
Group 9. Dwarf; herbaceous shoots; 10 taxa				
E. bubalina Boiss.	Osteoid	36.9±2.2	5.2	5.8
Group 11. Dwarf; tuberculate stem; thorny; 3 taxa				
E. fasciculata Thunb.	Osteoid	37.0±5.7	8.0	15.3
Group 12. Dwarf; short, tuberculate branches; 1 taxon				
E. clavarioides Boiss.	Osteoid	28.0±3.1	5.0	11.4
Group 13. Dwarf; caudex with tuberculate branches; 7 taxa				
E. woodii N.E. Br.	Spindle	28.9±2.4	5.2	3.6
Group 14. Dwarf; crown of tuberculate branches; 19 taxa				
E. davyi N.E. Br.	Osteoid(b)	31.8±4.0	6.2	13.1
E. maleolens Phill.	Osteoid	30.2±4.6	5.5	7.6
Group 15. Dwarf; numerous tuberculate branches; 24 taxa				
E. albertensis N.E. Br.	Osteoid	31.6±4.6	7.1	11.5
E. melanohydrata Nel	Osteoid(1)	33.4±5.6	6.8	12.9
Group 17. Dwarf; globose branches; 6 taxa				
E. globosa Sims.	Osteoid(b)	39.3±7.5	6.9	12.0
Group 18. Dwarf; columnar often angular branches; 9 taxa				
E. obesa Hook. f.	Osteoid	31.6±5.0	6.7	6.6
E. susannae Marl.	Osteoid	29.2±2.4	5.2	7.9
E. valida N.E. Br.	Osteoid	33.4±8.7	6.9	8.1
Group 19. Dwarf; shoot tuberculate, angled; thorny; 21 taxa				
E. aggregata Bgr.	Osteoid	29.3±4.6	6.9	10.3
E. pentagona Haw.	Osteoid	35.0±4.2	6.6	10.8
Group 20. Shrubs; leafy round or ribbed branches; thorny; 22 taxa				
E. capuronii U. and L.	Osteoid	27.5±2.1	5.3	11.4
E. decaryi Guill.	Osteoid	38.8±2.6	5.2	14.9
E. delphinensis U. and L.	Osteoid(b)	22.3±3.2	6.7	13.2
Group 21. Shrubs; fleshy leafy stems; 8 taxa				
E. sudanica Chev.	Osteoid	29.8±7.1	10.1	15.1
E. trapaeifolia Chev.	Osteoid	30.0±6.3	6.9	12.5
Group 22. Dwarf; several angled branches; thorns; 17 taxa				
E. groenewaldii Dyer	Osteoid	31.9±2.5	6.2	14.3
E. persistens Dyer	Osteoid(1)	30.2±2.5	5.0	11.8
Group 23. Trees; elongated angled stems; 3 taxa				
E. nyikae Pax	Osteoid	35.9±6.0	5.9	11.5
Group 24. Shrubs; branches 3–13 angled; leafy; thorns; 72 taxa				
E. acrurensis N.E. Br.	Osteoid(1)	28.6±2.6	6.6	13.4
E. echinus Hook. and Coss	Osteoid(1)	29.1±4.6	7.6	12.6
Group 25. Shrubs; branches rounded, tuberculate; thorns; 6 taxa				
E. unispina N.E. Br.	Osteoid	21.6±3.4	5.7	7.2
Madagascan (ankarensis) group				
E. francoisi Leandri	Osteoid(1)	32.6±2.4	5.3	13.6
Madagascan (perrieri) group				
E. didiereoides Denis	Osteoid(b,1)	44.2±5.2	8.5	24.7



Tentatively identified compounds include: A = campesterol; B = stigmasterol; C = ergosterol; D = euphol; E = tirucallol; F = sitosterol; G = β-amyrin; H = germanicol; I = cycloartenol.

Symbols: b, branching; 1, lobed.

other taxa. No evident relationship was apparent between length and shape; the small grains in *E. unispina* were somewhat osteoid in shape, while the small grains in *E. delphinensis* were highly osteoid. Similarly, the long grains in *E. ecklonii* were only somewhat osteoid, while those in *E. tirucalli* L. (group 4) as well as several other taxa (groups 11, 21, Madagascan) were highly osteoid.

Three general classes for grain length appeared evident (Table 1). Latex from many taxa contained starch grains approximately 30,0 to 34,0 µm long in different groups. No significant differences in length were evident between these taxa, and thus the 30,0 to 34,0 µm range represented a distinctive class for starch grains. There is also a class of grains of short length (20,0–24,0 µm) and a class of long length (40,0 µm or greater).

Even within a group, starch grain length can differ significantly between taxa (Table 1). This point is evident in group 4 in which the starch grains of *E. tirucalli* are in the long class whereas those of *E. fiherenensis* Poiss. and *E. xylophylloides* Brongn. are of intermediate length. In group 20 the starch grains of *E. delphinensis* are in the short class whereas other examined taxa possess grains of intermediate length.

Starch grain morphology also can differ within a group (Table 1). In group 18 the three taxa possessed somewhat osteoid grains as evidenced by the relationship of midregion to end width. However, in other groups the degree of grain osteoidy differed appreciably among the representative taxa (groups 1, 4, 14, Madagascan).

Starch grains also can develop branches at their midregion, as exemplified in several groups (symbol b). This trend can be observed among a number, but not all, grains in a population for a taxon. In latex from taxa possessing highly osteoid grains, the enlarged ends of some grains of the population may undergo lobing (symbol 1) to form grains of complex shapes (groups 15, 22, 24, Madagascan).

The triterpene (sterol) composition yielded characteristic profiles for each taxon (Table 1). Approximately 60 compounds, each with a specific retention time (RT), were detected in the profiles from each of the 38 examined taxa (closed circles in Table 1). Information on peak height and position for each chromatographic profile provided qualitative and quantitative data on triterpenes for a taxon as illustrated for *E. neohumberti* Boit. (Fig. 1). Few low or high molecular weight compounds other than triterpenes were present in the acetone extracts of latex. The number of triterpenes in the profile of a taxon ranged from as few as 2 in *E. groenewaldii* Dyer (group 22) to 14 in *E. didiereoides* Denis (Madagascan group).

Qualitative comparison of the complete profile from one group with that in another group showed little or no similarity (Table 1). One or several compounds may be similar between different groups. For example, euphol (RT 13,69 or compound D in Table 1) was present in taxa in a number of groups (exemplified by 4, 17, 21), but few other compounds were common between these groups. Even groups with a small number of compounds, as groups 13, 15 and 22, appeared not to have compounds with similar retention times.

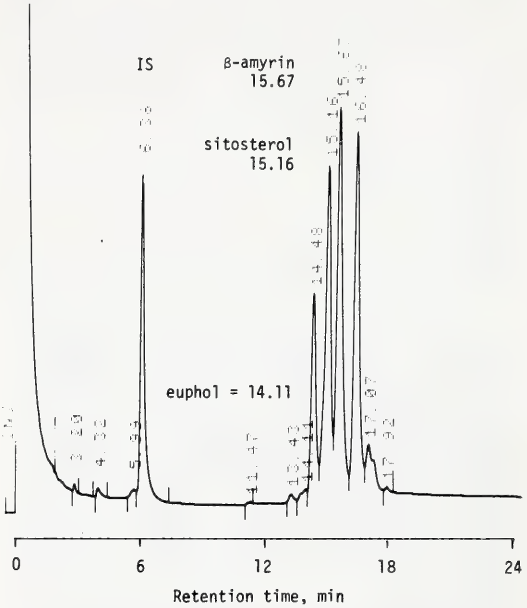


FIG. 1.—Chromatogram of *E. neohumberti* illustrating the several triterpene peaks present in the acetone extract of latex. IS is the internal standard. Euphol, sitosterol and β–amyrin are present in the latex, whereas compounds represented by the other peaks require identification.

Taxa within a group often contained few or no similar compounds as exemplified by groups 1, 7, 19, 24, or the Madagascan group. Taxa in several groups possessed similar compounds (as in groups 2, 4, 18, 20), yet each taxon differed by the presence or absence of one or more specific compounds. Several of these compounds have been identified (compounds are identified by letters A to I in Table 1), whereas other compounds require identification.

Taxa in several groups contained similar triterpene profiles. In group 2 the peaks with RT 14 through 18 were similar, but the taxa can be distinguished from each other by peaks in the area with RT 11 to 14. Only several components can be identified at this time including euphol (RT 13,69) and β–amyrin (RT 15,24). In group 4, represented by *E. fiherenensis, E. tirucalli,* and *E. xylophylloides,* euphol (RT 13,69) and tirucallol (RT 14,35) are common compounds, whereas the remaining components of the profile distinguish between these taxa.

Quantitative differences between the several components in a profile were apparent for each taxon and were evident as differences in chromatographic peak height and area. The ratio of compounds to each other, as represented by the prominent euphol and tirucallol components in *E. tirucalli* was similar for different samples.

Quantitative differences were evident for the same compound when it was present in different taxa. For example, in group 4 euphol and tirucallol were present in each of the taxa *E. fiherenensis, E.*

TABLE 2.—Percentage composition of sterols as components of the profile from taxa of group 4

Taxon	Euphol	Tirucallol	Unknowns		
			1	2	3
E. fiherenensis Poiss.	58.4	38.8	1.6	1.2	–
E. tirucalli L.	73.9	24.1	2.0	–	–
E. xylophylloides Brongn.	68.8	22.7	4.0	2.2	2.3

tirucalli, and *E. xylophylloides.* Euphol was the most abundant sterol in each taxon, 58,4%, 73,9% and 68,8% respectively, whereas tirucallol was present in lesser quantities, 38,8%, 24,1%, and 22,7% respectively (Table 2). The other components of the profile indicated as unknowns also occurred in different ratios within these taxa; further studies will be necessary to identify these triterpenes. Importantly, each taxon possessed characteristic quantities of particular compounds which aided to separate the several taxa.

Coinjection of different external standards with the samples from *E. obesa* Hook. f. tentatively identified sitosterol and β–amyrin among the eight components of the profile. Similar studies as well as those integrated with mass spectrometry are necessary to ascertain the identity of compounds in this and other taxa.

DISCUSSION

Latex exudate from laticifers in *Euphorbia* contained plastids and numerous triterpenes. This laticifer type is present in only a few dicotyledonous families including Euphorbiaceae, and the unusual characters of this cell type indicate it to be of recent evolutionary origin (Mahlberg, 1975; Mahlberg & Sabharwal, 1967, 1968). These starch grains have been reported in the early literature (Gaucher, 1902; Marloth, 1913–32), as have been the presence of triterpenes (Haines & Warren, 1949). The genetical control of starch grain morphology in plastids and the patterns of triterpenes (sterols) in the laticifer represent stable traits associated with the phylogeny of a taxon (Biesboer, 1979; Mahlberg, 1982).

Starch grains from laticifers can aid to distinguish between groups of taxa in this genus. Both grain morphology and length can be utilized to evaluate interspecific relationships between taxa. Rod and spindle shaped grains, which characterize leafy taxa in several subgenera uncommon on the African continent (Biesboer & Mahlberg, 1981) are interpreted to be less specialized than osteoid grains. Progressive specialization of starch grains is associated with increased length for the several grain types. Starch grains somewhat osteoid in form, present in taxa from dwarf groups, are interpreted to be less specialized than those starch grains with much enlarged ends. This pattern of starch grain phylogeny may also reflect the trend of specialization for these taxa. Taxa in dwarf groups differed within and between groups for the features of starch grain size and form, although they appeared to represent groups intermediate in specialization among the *Euphorbia.* Grains with enlarged and lobed ends, as observed for Madagascan taxa, are interpreted to represent phylogenetically derived taxa. The occurrence of rod shaped starch grains in several African taxa requires further study. This condition may represent a secondarily derived condition involving loss of a capacity to develop the osteoid feature.

The triterpene (sterol) profile of latex was found to be quantitatively and qualitatively distinctive for a taxon and comparable to a fingerprint for the taxon. Our studies support the interpretation that these compounds represent unique biological markers which can be employed to advantage to identify and correlate phylogenetic relationships between taxa of this genus.

It has been reported that latex sterol composition of a taxon was stable under different conditions and from different cultivars of a species (Biesboer, 1979; Biesboer *et al.,* 1982). Latex triterpenes have been utilized previously to interpret relationships between taxa of *Euphorbia* (Ponsinet & Ourisson, 1965, 1968; Anton, 1974; Biesboer, 1979). These authors described different groups of *Euphorbia* reflective of their major triterpenes to provide a chemotaxonomic interpretation of this genus.

The development of gas-liquid chromatography, such as we employed, has provided a highly sensitive technique to obtain quantitative and qualitative data on the numerous components in latex. Importantly, the degree of affinity between taxa is reflective of the number of identical compounds present among the components of the profile and the relative quantity of similar components when present in different taxa. Thus, examined taxa within groups 2 and 4 represent more natural groupings than do taxa within other groups (as 7 and 24).

A high number of triterpenes in latex is interpreted to represent a derived condition, and is noted for some Madagascan taxa. The fewest number of triterpenes was noted in taxa from several dwarf groups although other taxa among the dwarf groups had a greater number of sterols as did taxa in groups containing shrubby and arborescent taxa. As a generalization both the starch grain and triterpene data support an interpretation that Madagascan taxa represent a derived condition.

Further studies are necessary on the mechanism and genetic processes controlling the features of starch grain morphology and triterpene formation in the laticifer. Studies indicate that the numerous variations of each feature are derived by gene mutation resulting in the formation of several morphological forms of starch grain and numerous triterpene compounds without altering species survival ability. Integration of data on these two features which represent stable markers from the laticifer will provide insight into the phylogeny of this complex genus and will aid to develop more natural groupings than exist currently.

ACKNOWLEDGEMENTS

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Phytogeography and interspecies relationships in *Monsonia* (Geraniaceae)

H. J. T. VENTER*

ABSTRACT

The geographical distribution of *Monsonia* and its 25 species is examined. It is shown that the genus inhabits various climatic regions (desert, semi-desert, savanna and temperate grassland) of Africa, south-west Asia and Madagascar. Attention is also paid to the interrelationships of the *Monsonia* species in comparison to their distribution patterns. Possible links between the species of southern Africa and those of northern Africa are also discussed.

RÉSUMÉ

LA PHYTOGÉOGRAPHIE ET LES RELATIONS INTERSPÉCIFIQUES DE MONSONIA *(GERANIACEAE)*

La répartition géographique de Monsonia *et des ses 25 espèces est examinée. Il est montré que le genre habite des régions climatiques variées (désert, semi-désert, savanne et formation herbeuse tempérée) de l'Afrique, du Sud-Ouest asiatique et de Madagascar. Une attention est aussi accordée aux relations entre les espèces de* Monsonia *en comparaison avec leur mode de distribution. Les liens possibles entre les espèces d'Afrique australe et celles d'Afrique du Nord sont aussi discutés.*

INTRODUCTION

Monsonia is one of five genera recognized in the Geraniaceae (Hutchinson, 1969). The character in common to the five genera and which is distinctive for the family, is the schizocarp fruit which, at maturity, divides into five mericarps.

The family is dispersed over both hemispheres in Africa, America, Europe, Asia and Australia.

Hutchinson (1969) claims that the main centre of distribution of the Geraniaceae is southern Africa where all the genera excepting *Erodium* L'Hérit. are abundant to very abundant. White (1971), however, warns that major climatic changes swept over Africa since the separation of the continents and that these changes were certain to have had important impact on the distribution of plant families.

Monsonia is a genus of 25 species (Venter, 1979). The species are rather uniform in morphology, especially with respect to their floral structure. The genus is distinguished from the other four genera in the family by having actinomorphic flowers with 15 stamens and by being herbaceous.

DISCUSSION

Monsonia is found in Africa, Madagascar and south-west Asia as far east as Pakistan and India. The main concentration of species occurs in southern Africa where 21 species are found, of which 18 are endemic to the region. Two species are endemic to east Africa. Another two are endemic to the Sahara and Sind deserts.

Ecologically *Monsonia* inhabits a variety of niches. A number of species are found in deserts (Namib, Sahara and Sind deserts), several occur in semi-desert areas, whereas another group inhabits subtropical or tropical bushlands or grasslands which may be dry or moderately moist. A small number, mainly weedlike annuals with wide ecological amplitudes, are encountered over large areas under a variety of climatic conditions. A few species are found in high altitude temperate grassland. One species occurs only in the winter rainfall south-west Cape of South Africa.

Two sections may be distinguished, viz. *Plumosae* Boiss. and *Barbatae* Boiss.. They are distinguished from each other not only by the structure of the mericarp, but also by the free or connate sepals and the presence or absence of sepal spurs (Fig. 1).

Section **Plumosae:**

Diagnostic features: Prostrate or decumbent suffrutescent herbs, some members with erect rhizomes. *Leaves* broadly ovate to orbicular, venation palmate. *Inflorescenses* 1–14-flowered. *Sepals* mostly connate and spurred at their bases. *Petals* obtriangular, obovate or elliptic. *Stamens* in a cylindrical column around the gynoecium. *Mericarps* obconical with the tail in most of the members plumose.

Plumosae comprises 11 species, viz. *M. deserticola* Dinter ex Knuth, *M. drudeana* Schinz, *M. heliotropioides* (Cav.) Boiss., *M. ignorata* Merxm. & Schreiber, *M. longipes* Knuth, *M. luederitziana* Focke & Schinz, *M. nivea* (Decne.) Webb, *M. parvifolia* Schinz, *M. speciosa* L., *M. trilobata* Kers and *M. umbellata* Harv.

The members of *Plumosae* inhabit deserts and semi-deserts at altitudes between sea-level and approximately 1 700 m above sea-level (Figs 2 & 3). *M. speciosa* and *M. longipes* are the two exceptions, being found in the winter rainfall area of the south-western Cape in South Africa and the highlands of eastern Africa respectively.

Seven species are endemic to the Karoo-Namib Region. Two are endemic to the Mediterranean and

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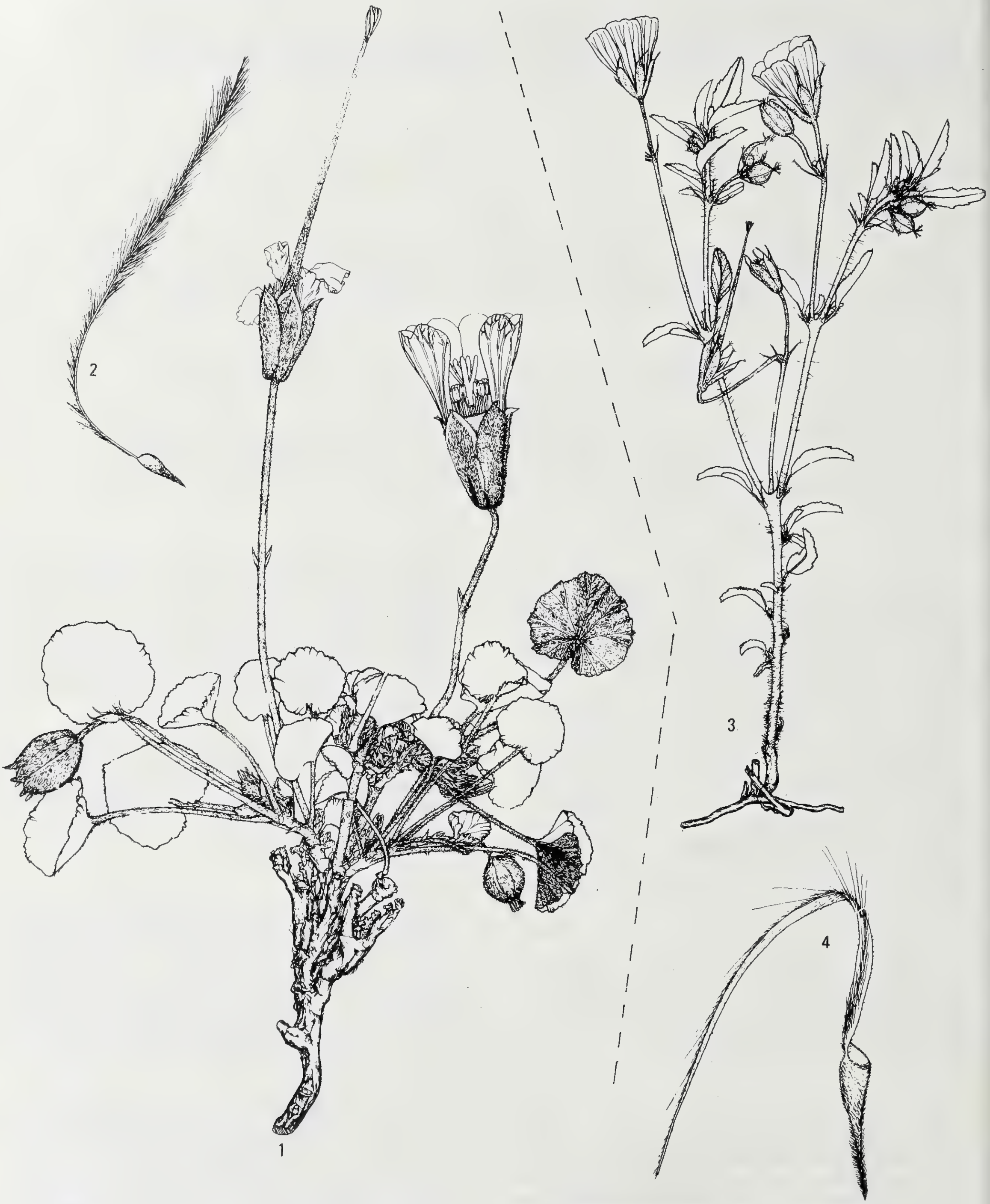

FIG. 1.—*Monsonia drudeana* of section *Plumosae:* 1, habit, × 0,75; 2, mericarp with plumose tail, × 2. *M. burkeana* of *Barbatae*: 3, habit, × 0, 75; 4, mericarp with crested tail.

Saharo-Sindian Regions of north Africa and south-west Asia.

M. deserticola, M. drudeana and *M. ignorata* inhabit the southern part of the Namib Desert in SWA/Namibia. Extremely arid conditions prevail here. The little precipitation is derived from fog and winter rain. The habitat varies from windswept sand dunes to sandy river washes. All three species are perennial and possess orthotropous subterrestrial rhizomes. *M. speciosa* is the only other species in *Monsonia* that has a rhizome and, although it does not inhabit desert, it also grows in a sandy habitat and has to withstand long, dry summers by remaining dormant subterrestrially.

In the vast semi-desert Karoo north, east and south of the Namib Desert proper four more species are found. They are all endemic to the area and comprise *M. leuderitziana, M. parvifolia, M. umbellata* and *M. trilobata.* The first three species are in all respects closely related. They are also related to *M. drudeana* through their identical pollen (Venter, 1980). In contrast to *M. luederitziana, M. parvifolia* and *M. umbellata* which are widely distributed over the area, *M. trilobata* is restricted to a very small area in South West Africa/Namibia on the eastern border of the Karoo-Namib Region. Although it belongs to the *Plumosae* of the Karoo-Namib, its relation to the other members is not clear.

The position of *M. ignorata* within the group is also unclear. Although it resembles *M. drudeana* vegetatively, its flower, pollen and fruit differ markedly. *M. deserticola* differs even more with distinct, spurless sepals.

M. heliotropioides and *M. nivea* inhabit the Mediterranean and Saharo-Sindian Regions of north Africa and south-west Asia as far east as Pakistan and the western border of India (Figs 2 & 3). They are very similar in appearance and are obviously closely related, especially on account of their distinctive type of pollen (Bortenschlager, 1967; Venter, 1980). They are distinguishable from the Karoo-Namib species because of their very small

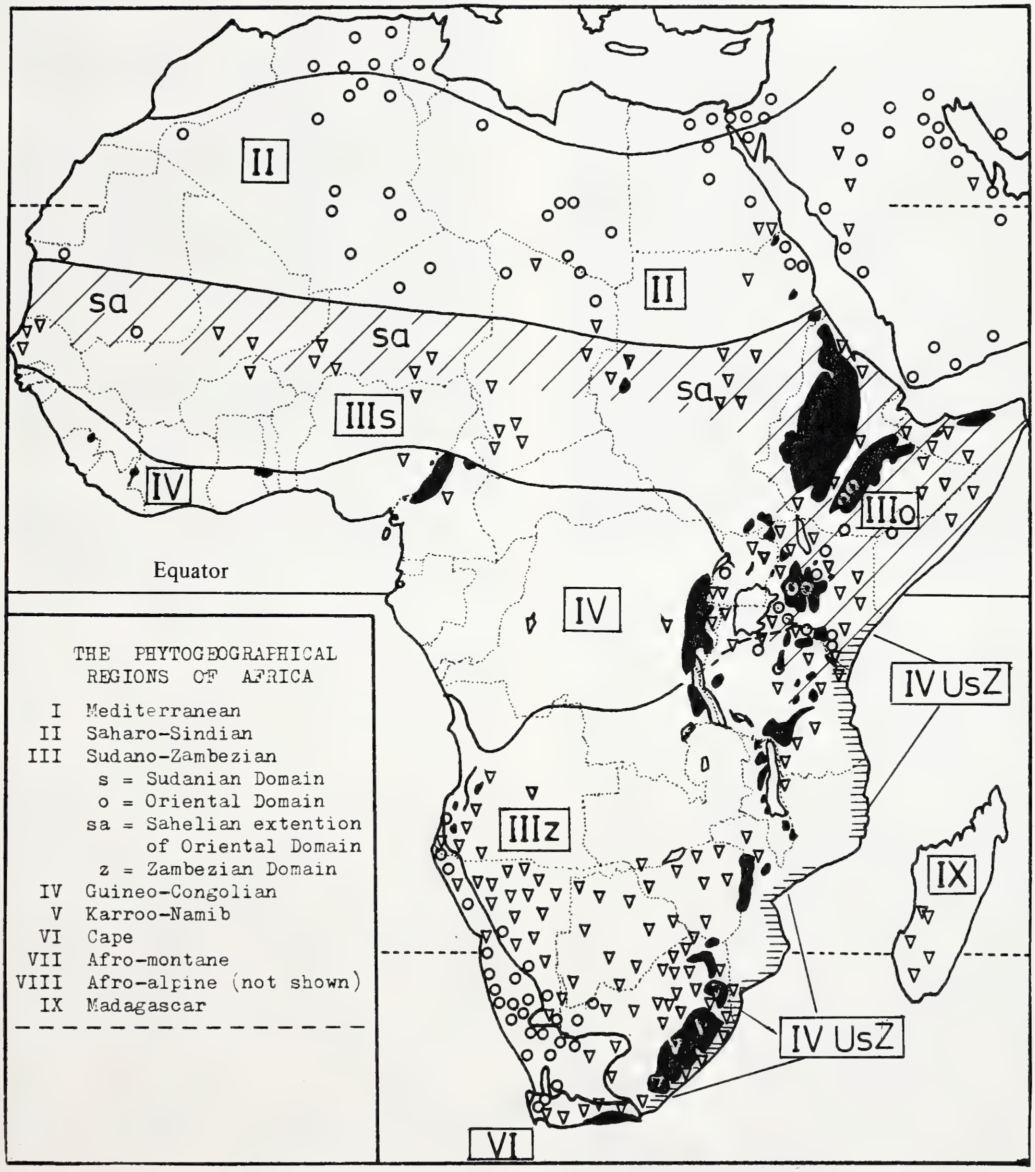

FIG. 2.—The geographical distribution of *Monsonia* and its sections, *Barbatae* (▽) and *Plumosae* (O) in Africa (map after White, 1971).

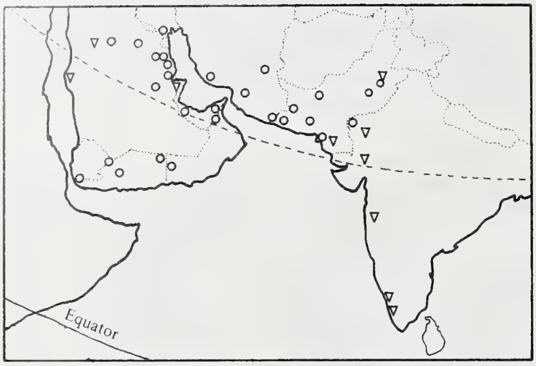

FIG. 3.—The geographical distribution of *Monsonia* and its sections, *Barbatae* (▽) and *Plumosae* (O) in south-west Asia.

flowers bearing only eight relatively large pollen grains per anther cell, and by their pollen sculpture.

M. deserticola, the 'odd' species in the Karoo-Namib Region resembles *M. heliotropioides* and *M. nivea* to quite a degree, especially in the size and form of the flower. If the distance separating *M. deserticola* from *M. heliotropioides* and *M. nivea* was not known, one would be tempted to group these three species together.

Considering this resemblance and the overall discontinuous geographical distribution of *Plumosae,* the question arises whether a link exists between the Karoo-Namib and the Saharo-Sindian species. At present no climatic link exists between these two widely separated regions which would explain a possible link. Was there a former link? De Winter (1966) writes: 'It is evident from the large number of species which occur unchanged in the northern and southern areas that the possibility of a former link between these areas must be considered'. Winterbottom (1967) suggests 'that at some period in the past, there must have been a corridor of desert or semi-desert country across central Tanganyika (Tanzania) and through Zambia linking the Somali Arid and the South West Arid Districts of today' and 'that these conditions obtained more than once'. Van Zinderen Bakker Snr (1969) proposes that this corridor probably existed in periods of higher temperature. Verdcourt (1969) discussed the possibility that such a corridor stretched from the south-west to the north-east and henceforth to Sind and Rasjasthan in South-West Asia. It is important to note that he states that even during the wettest periods in Africa the climate of South-West Africa and Somalia never became wetter than semi-arid, that these two areas acted as refuges for desert plants and that these areas, moreover, acted as evolutionary centres of desert plants. It is also of importance that Van Zinderen Bakker Snr (1975) regards the taxonomic affinities between the proper hyper-arid Namib biota and the Sahara-Sindic elements as very old.

M. speciosa and *M. longipes,* the two non-desert species of *Plumosae* correspond to a large degree in vegetative and floral morphology, but they are separated by some 5 000 km, *M. speciosa* being from the Cape in South Africa and *M. longipes* from Kenya, Ethiopia and Tanzania in eastern Africa. As was the case with the desert elements, the question is whether a link exits or existed between these two species. The arid corridor, already mentioned, may have been the link, but both species are more temperate in character, although *M. speciosa* reveals xeromorphic trends. An alternative, cool, humid link via the mountains along the eastern part of Africa may have existed in the past (Bader, 1965; Van Zinderen Bakker Snr, 1970; Coetzee, 1978), but at present this route is certainly disjunct because of hot arid barriers such as the Limpopo and Zambezi Valleys.

Section **Barbatae:**

Diagnostic features: Prostrate, decumbent or erect perennial or annual herbs. *Leaves* linear, ovate or elliptic; venation linear to subpalmate. *Inflorescenses* 1–3–(4)-flowered. *Sepals* free. *Petals* obtriangular. *Stamens* arranged in a cup-shaped column around the pistil. *Mericarps* obliquely obovoid with their tails crested at the base.

Barbatae comprises *M. angustifolia* E. Mey. ex A. Rich., *M. attenuata* Harv., *M. brevirostrata* Knuth, *M. burkeana* Planch. ex Harv., *M. emarginata* (L.f.) L'Hérit., *M. galpinii* Schltr. ex Knuth, *M. glauca* Knuth, *M. grandifolia* Knuth, *M. lanuginosa* Knuth, *M. natalensis* Knuth, *M. praemorsa* E. Mey. ex Knuth, *M. senegalensis* Guill. & Perr. and *M. transvaalensis* Knuth.

Barbatae is distributed over a large part of Africa, but its main concentration is found in the Zambezian Domain and Afromontane Region of southern Africa (Fig. 2). Only four species of *Barbatae* are found north of the equator and of these only one is endemic to the region.

The most widely dispersed species in *Monsonia* belong to *Barbatae.* These are *M. angustifolia, M. glauca* and *M. senegalensis. M. angustifolia,* an annual weed, occurs throughout most of Africa and also in Madagascar. It is adapted to a very wide range of environmental conditions that include semi-desert scrub veld, savanna, humid subtropical scrub and tropical to temperate grassland. Altitudinally its habitat ranges from sea-level to 2 500 m above sea-level. *M. glauca* is encountered in hot semi-arid karoo veld to savanna from southern Africa to Kenya and Tanzania in east Africa. *M. senegalensis* has by far the widest distribution of all the species of *Monsonia.* It is found from the Zambezian Domain in southern Africa to the Oriental Domain of eastern Africa and along its Sahelian Extension to west Africa (Fig. 2). It is, however, also present in south-west Asia from Arabia to West Pakistan and India (Fig. 3). This annual species inhabits hot semi-arid veld and dry savanna or scrub veld from sea-level to about 1 600 m above sea-level.

M. ignea is endemic to the arid bush country of Ethiopia and Somalia in the horn of Africa. It seems to form a natural group together with *M. senegalensis* and *M. glauca.*

All other members of *Barbatae* are restricted to southern Africa.

M. burkeana, M. praemorsa and *M. natalesis* are predominantly found in subtropical bushveld.

M. attenuata, M. lanuginosa and *M. transvaalensis* are quite similar in appearance and are found in grassland of mountain sides or highveld areas above approximately 1 300 m above sea-level. Although *M. brevirostrata* is encountered in the same habitat as the above three species, it is not related to these species, but rather to *M. angustifolia.*

M. emarginata, M. grandifolia and *M. galpinii* are related. They inhabit coastal scrub and lower altitude mountain grassland in the Cape Region and the Usambara-Zululand Domain (Fig. 2). *M. galpinii* has the smallest range of distribution of any species in *Monsonia.* It is found only in a very restricted area in coast dune scrub at East London in South Africa.

The vague interrelationships of such a high proportion of species in *Monsonia,* especially in *Barbatae* which is the more primitive section of the genus (Venter 1980), may perhaps be due to the present species being isolated remnants of a once richer assortment of species with wider and more confluent distribution over Africa. The climatic changes that have oscillated over Africa since the drift of the continents may have impoverished the genus, resulting in the rather unrelated assortment of today. Very few specimens exist which may be regarded as hybrids and this may also indicate that the present day species are not closely related genetically. The very small distribution areas and the scarcity of specimens in some of the species may also indicate that these members of *Monsonia* are becoming extinct, although one must always keep in mind that the opposite may be as true. *Monsonia,* however, exhibits some of the most primitive characteristics in the Geraniaceae (Moffett, 1978; Venter, 1980) from which the assumption may be made that it belongs to the oldest stock of the family and may therefore be less active in speciation today.

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Analyse de la répartition géographique des Malphigiaceae d'après les caractères du pollen et de la pollinisation

D. LOBREAU-CALLEN*

RÉSUMÉ

Une étude comparative du pollen et de la pollinisation des Malphigiaceae montre que les genres de l'Ancien Monde sont dérivés de ceux d'Amérique du Sud. Ils sont représentés sur ces continents depuis le Crétacé. En Amérique du Sud il y a eu coadaptation entre les caractères du pollen et les insectes pollinisateurs strictement représentés sur ce continent et donc diversifiés postérieurement à l'élargissement de l'Atlantique (Tertiaire).

Les caractères polliniques des Malphighiaceae permettent les rapprochements avec ceux des pollens des autres familles des Polygalales; ils se rapprochent palynologiquement des Euphorbiaceae d'une part et des Légumineuses comme des Rutales–Sapindales d'autre part.

ABSTRACT

ANALYSIS OF THE GEOGRAPHICAL DISTRIBUTION OF MALPHIGIACEAE USING POLLEN AND POLLINATION CHARACTERS

A comparative study of pollen and pollination in the family Malphigiaceae shows that the genera of the Old World are derived from those in South America. They have existed on the continents involved since the Cretaceous.

In South America there is coadaptation oetween the pollen characters and the pollinating insects present only on this continent and subsequently diversified after the enlargement of the Atlantic in the Tertiary.

Pollen characters of the Malphigiaceae show affinities with those of other families of the Polygalales. Palynologically, Malphigiaceae approaches Euphorbiaceae on the one hand, and Leguminosae and Rutales–Sapindales on the other.

INTRODUCTION

La famille pantropicale des Malphigiaceae est largement répandue en Afrique et à Madagascar, dans les régions tropicales et subtropicales, où elle est représentée par une quinzaine de genres.

Les Malpighiaceae présentent plusieurs caractères morphologiques qui varient d'un genre à l'autre: nombre de pièces florales avec en particulier une tendance à la zygomorphie et à la réduction du nombre d'étamines, fleurs chasmogames et cléistogames (Niedenzu, 1928; Anderson, 1980), acquisition de glandes calicinales sécrétrices d'huiles (Vogel, 1974), nombreux types polliniques (Lobreau 1966 à 1968, Lobreau-Callen, 1974–1975). De même certains caractères cytologiques sont différents selon les genres: type de noyau, nombre chromosomique (Fouët, 1966; McBryde, 1970). La pollinisation des Malpighiaceae est effectuée par des Hyménoptères et Vogel montrait en 1974 qu'il y a "coévolution" entre les caractères: morphologie florale — insectes pollinisateurs.

A la lumière de ces données nous allons tenter de préciser les rapports susceptibles d'exister avec la morphologie pollinique.

Plusieurs classifications des Malphigiaceae sont actuellement en présence. La première est celle de Niedenzu (1890) reprise par Arènes (1959) où la famille est scindée en deux sous-familles:

Les *Pterygophorae* avec quatre tribus:

— Les *Hiraeeae* avec les *Mascagniniinae* pour les genres du Nouveau Monde, en général, et les *Aspidopteryginae* pour les espèces de l'Ancien Monde,

—Les *Banisterieae* avec les *Banisteriinae* pour les genres du Nouveau Monde, en général, et les *Sphedamnocarpinae* pour ceux de l'Ancien Monde,

—Les *Tricomarieae* intégralement sud-américaines,

—Les *Rhynchophoraeae* avec un seul genre à Madagascar.

Les *Apterygiae,* sous-famille sud-américaine, sont également divisées en deux tribus:

—Les *Galphimieae* avec les *Galphimiinae* et les *Bunchosiae,*

—Les *Malpighieae* avec les *Malpighiinae* et les *Byrsonimiinae.*

Cette classification a été modifiée par Niedenzu en 1928 où les *Planitorae* remplacent les *Apterygiae* et les *Pyramidotorae,* les *Pterygophorae.* Pour Norton (1968) les noms proposés par Niedenzu ne sont pas valables et il propose les *Malpighioideae* pour les *Planitorae* et les *Gaudichaudioideae* pour les *Pyramidotorae.* Plus récemment Anderson (1978) proposait une nouvelle classification malheureusement partielle encore à ce jour. Il rassemble les genres à fruits véritablement aptères dans la sous-famille des *Byrsonimoideae* et pense rapprocher des *Gaudichaudioideae* les genres *Bunchosia, Clonodia, Dicella, Heladena, Malpighia, Thryallis* généralement classés parmi les genres à fruits totalement aptères, alors qu'en fait ces derniers sont dérivés de fruits ailés.

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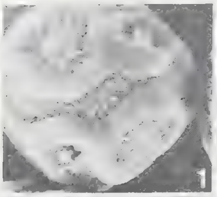
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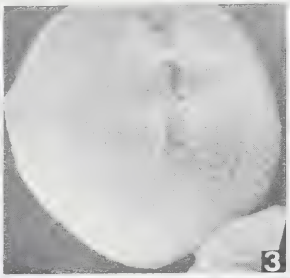
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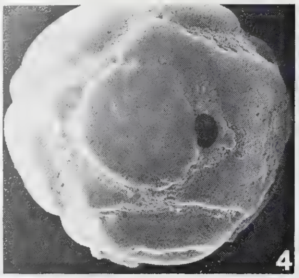
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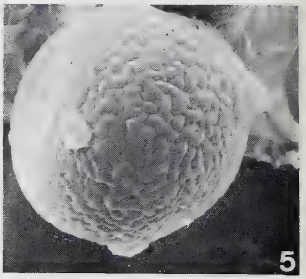
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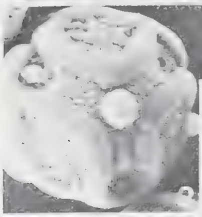
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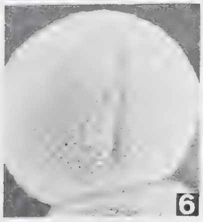
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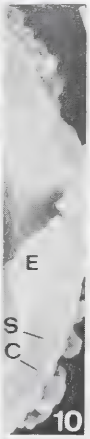

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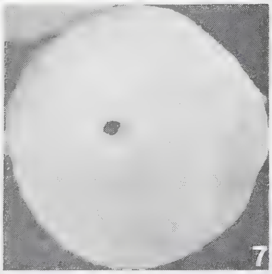
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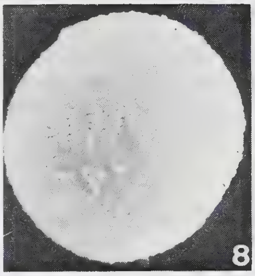
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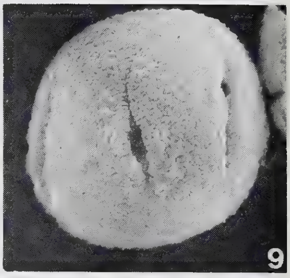
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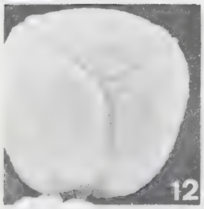
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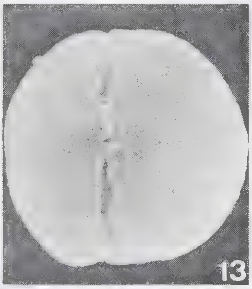
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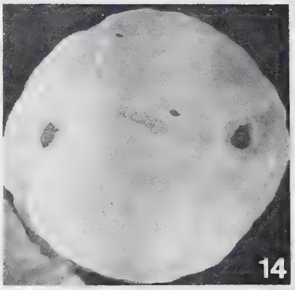
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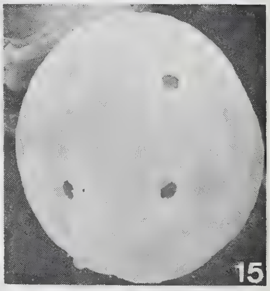
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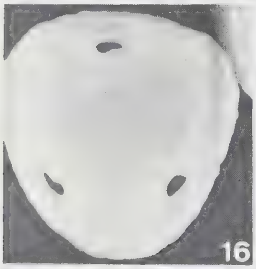
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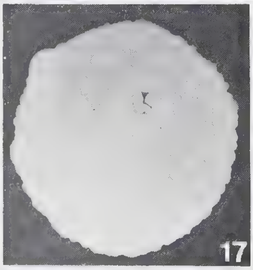
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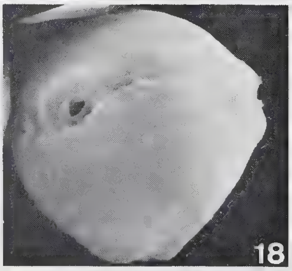
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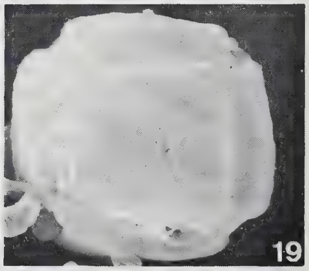
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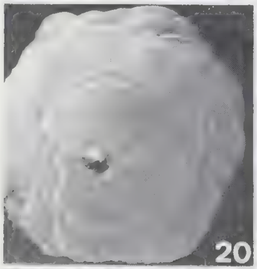
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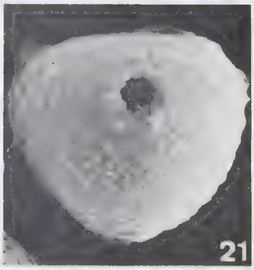
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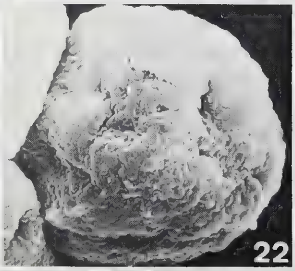
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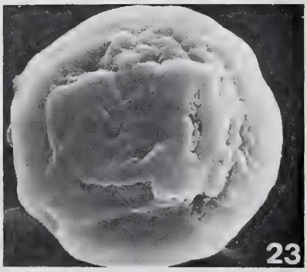
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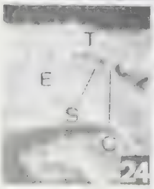

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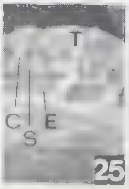

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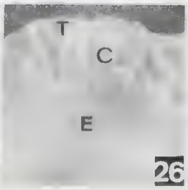

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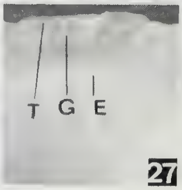

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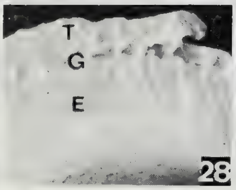

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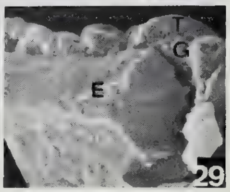

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FIG. 1 (Opposite page).—1–2, *Aspicarpa linearifolia* (St. Hil.) Ndz.: 1, grain cubique dont l'axe polaire est vertical, × 720; 2, vue polaire, × 720. 3. *Lophanthera lactescens* Duke, aperture, × 3 000. 4, *Malpighia galeottiana* A. Juss. pore et sillons vestigiaux, × 1 000. 5, *Bunchosia media* DC., pores, × 2 000. 6, *Byrsonima* sp., aperture, × 3 000. 7, *Heladena bunchosioides* (A. Juss.) A. Juss., endoaperture et pore vestigial, × 2 000. 8, *Rynchophora humbertii* J. Ar., × 2 000. 9, *Echinopterys eglandulosa* (A. Juss.) Small, disposition des endoapertures sur une spirale subéquatoriale, × 2 000. 10, *Lophanthera lactescens* Duke, coupe longitudinale de l'exine au niveau d'une aperture complexe, endexine perforée, épaissie autour de l'endoaperture, × 4 800. 11, *Rhynchophora humbertii* J. Ar., endexine endosculptée, × 4 000. 12, *Rhynopterys kerstingii* (Engl.) Ndz., vue polaire, syncolpie, × 2 000. 13, *Acridocarpus humbertii* J. Ar., apertures, × 3 000. 14, *Peixotoa jussieuana* Mast., pores et sillons vestigiaux, × 1 000. 15, *Tricomaria usilo* Guill. ex Hook. & Arn., 2 pores par sillons vestigiaux et brefs sillons vestigiaux dans chaque intercolpium. 16, *Triaspis hispida* Pierre ex Badré, au centre, facette avec un tectum rugulé, sur les côtés, facettes avec un tectum perforé, × 1 000. 17. *Sphedamnocarpus angolensis* (A. Juss.) Planch., pore, × 1 000. 18, *Tetrapterys citrifolia* Pers., vue polaire d'un grain triporé avec des sillons vestigiaux, × 2 000. 19, *Gaudichaudia cynanchoides* H.B.K. (fleur chasmogame), intercolpium, × 2 000. 20, *Hiptage madablota* Gaertner, pore de face et épaississements, × 1 500. 21, *Tristellateia africana* S. Moore, pore, × 2 000. 22, *Aspicarpa hartwegiana* A. Juss. (fleur cleistogame), × 1 300. 23, *Gaudichaudia cynanchioides* H.B.K. (fleur cleistogame), × 1 000. 24–29, structure de l'exine chez: 24, *Rhynopterys kertingii* (Engl.) Ndz., × 10 000; 25, *Echinopterys eglandulosa* (Juss.) Small, × 10 000; 26, *Peixotoa jussieuana* Mast., × 10 000; 27, *Tricomaria usilo* Guill. ex Hook. & Arn., × 6 000; 28, *Banisteriopsis elegans* (Tr. & Pl.) Sander subsp. *cordata* (Ndz.) Sander var. *pulcherrima* Sander, × 10 000; 29, *Hiptage madablota* Gaertner, × 8 000. (C = columelle; E = endexine; G = grains; S = sole; T = tectum.)

Notre travail est présenté en utilisant la classification de Niedenzu de 1890, mais dans un chapitre spécial nous dicuterons nos résultats avec ceux d'Anderson.

CARACTÈRES POLLINIQUES

Les pollens des Malpighiaceae ont fait l'objet de nombreuses études souvent fragmentaires (cf. Index bibliographique, Thanikaimoni, 1972–1980). Depuis (1966) nous avons étudié le pollen des Malpighiaceae d'Afrique et de Madagascar tant au microscope photonique qu'au microscope électronique à balayage; grâce à l'observation de pollen au stade tétrade il nous a été possible d'orienter les eumonades des Malpighiaceae: les ectoapertures sont fréquemment syncolpées et (ou) parasyncolpées surtout lorsqu'elles sont vestigiales et ont une symétrie cubique; les endoapertures sont toujours subéquatoriales, souvent sur deux plans parallèles de part et d'autre de l'équateur, et sont disposées selon la loi de Fischer pour l'un des plans et la loi de Garside pour l'autre plan (pollens hexaporés). Les grains inaperturés sont sphériques et leur ornementation comme l'épaisseur de l'exine sont plus réduites à un pôle. Dans cette région, l'intine est plus épaisse. Il s'agit donc de la zone germinative *(Rhynchophora humbertii, Microsteira floribunda, Digoniopterys humbertii*).*

Genres d'Amérique

1. *Sous-famille* Apterygiae

Toutes les fleurs sont chasmogames, le pollen est de deux types, colporé ou poré avec ou sans sillons vestigiaux. Il est tricolporé dans les deux sous-tribus, *Galphimiinae p.p.* (Fig. 2.1 & 2.3) et *Byrsoniminae p.p.* (Fig. 1.6), parfois syncolporé *(Spachea p.p.,* sous-tribu *Galphimieae),* parasyncolpé *(Galphimia,* sect. *Cosmogalphimia).* L'ectoaperture peut être large, tendre à être vestigiale et divisée dichotomiquement aux extrémités (ex. *Lophanthera,* Fig. 1.3).

Les pollens colporés sont réticulés ou microréticulés *(Byrsonima,* Fig. 1.6; *Blepharandra; Burdachia; Lophanthera)* ou tectés, le tectum étant perforé *(Acmanthera, Coleostachys, Diacidia, Glandonia, MacVaughia, Pterandra, Spachea, Verrucularia),* la couche infratectale est columellaire, la sole moins épaisse que l'endexine (Fig. 1.10). Les pollens sont porés avec 4 ou 5 pores subéquatoriaux *(Heladena,* Fig. 1.7*)* ou 4 *(Thryallis)* ou 6 (*Bunchosia,* Fig 1.5*)* pores équidistants. Chez *Clonodia, Dicella* (Fig. 2.7–2.9) et *Malpighia* (Fig. 1.4), le pollen présente des sillons vestigiaux. Chez *Heladena* (Fig. 1.7), les sillons vestigiaux sont remplacés par des pores vestigiaux.

Le tectum est aréolé (ex. *Bunchosia,* Fig. 1.5) ou lisse, plus ou moins finement perforé chez *Malpighia* par exemple (Fig. 1.4); la couche infratectale est columellaire (ex. *Thryallis*) ou grenue (*Bunchosia, Malpighia,* Larsen & *al.*, 1962). La nexine n'est constituée que d'endexine (ex. *Malpighia*).

En conclusion, chez les *Apterygiae,* les pollens colporés ont une couche infratectale columellaire et un tectum largement perforé (discontinu), les pollens porés avec ou sans sillons vestigiaux ont une couche infratectale grenue ou columellaire. Lorsque cette couche est grenue, le tectum est lisse, rarement perforé (donc continu); lorsque la couche est columellaire, le tectum est largement perforé (donc discontinu).

2. *Sous-famille* Pterygophorae

(a) *Tribu des* Tricomariae

Les fleurs sont toutes chasmogames. Les pollens sont tous colporés. Seul *Tricomaria* présente un pollen poréavec de larges sillons vestigiaux lui donnant un aspect colporé (Fig. 1.15). Les endoapertures sont situées sur un plan équatorial chez les grains colporés (ex. *Lasiocarpus, Ptilochaeta*) ou disposés selon une spirale subéquatoriale (ex *Echinopterys,* Fig. 1.9). Chez *Tricomaria* les endoapertures au nombre de 2 par sillon sont disposées sur deux plans. L'exine est réticulée, simplicolumellée et la sole est moins épaisse que l'endexine chez les grains colporés (Fig.

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* Les pollens de ces deux genres décrits dans nos travaux antérieurs ne correspondent pas à ceux que nous avons observés lors de nos études récentes. Il s'agissait probablement de contaminations. Chez *Rhynchophora* (fleurs hermaphrodites) le pollen est inaperturé, verruqueux. Chez *Digoniopterys,* (étamines mûres d'une fleur femelle ou protogyne) le pollen morphologiquement fertile, est également inaperturé, tecté et perforé ou verruqueux.

1.25). Le tectum est lisse et la couche infratectale grenue repose directement sur l'endexine dans les grains à sillons vestigiaux (Fig. 1.27): *Tricomaria; Henleophytum.*

(b) *Tribu des* Banisteriae, *sous-tribu des* Banisteriinae

Les pollens sont porés et présentent des sillons vestigiaux. Les pollens des fleurs chasmogames sont généralement cubiques (ex. Figs 1.1 & 2.14), parfois sphériques. Selon les espèces du genre *Banisteriopsis,* soit les apertures vestigiales sont plus ou moins parallèles entre elles et ramifiées à une ou deux extrémités et les endoapertures subéquatoriales ou disposées sur deux plans (Fig. 2.4–2.6), soit les apertures vestigiales sont placées selon les arêtes d'un cube et les endoapertures sur deux plans. Le tectum est lisse et perforé ou rugulé au centre des faces du cube (ex. *Aspicarpa, Banisteria, Peixotoa* Fig. 1.1, 1.2 & 1.14) et la couche infratectale est granulo-columellaire (Fig. 1.26), les columelles étant très irrégulières et ayant l'aspect de gros grains. Le tectum est lisse et la couche infratectale grenue (ex. *Stigmatophyllum p.p., Banisteriopsis p.p.,* Fig. 1.28).

Les pollens des fleurs cléistogames (Fig. 1.23) sont subsphériques et porés. Les sillons vestigiaux sont plus ou moins fermés. Le tectum est lisse ou aréolé et la couche infratectale grenue, la nexine est très épaisse. L'aspect général du pollen paraît être celui des grains dont la maturité de l'exine (*sensu* Rowley & Dahl, 1977) ne serait pas atteinte alors que le gamétophyte était apte à la fécondation. D'ailleurs, dans un tel pollen, l'exine ne semble plus jouer aucun rôle, la germination ayant lieu dans l'anthère.

(c) *Tribu des* Hiraeeae, *sous-tribu des* Mascagniinae

Les caractères des fleurs chasmogames sont comparables à ceux de la sous-tribu précédente. Le pollen est toutefois généralement sphérique, parfois cubique (ex. *Gaudichaudia,* Fig. 1.19) et les sillons vestigiaux sont relativement plus courts ou nettement plus longs et étroits *(Hiraea).* Ils sont parfois absents (ex. *Tetrapterys crispa, Hiptage fagifolia*). Le pollen est octocolporé chez *Dinemandra.* L'exine est réticulée, simplicolumellée chez les pollens colporés; le tectum est lisse et la couche infratectale grenue (ex. *Mascagnia macradena*) ou le tectum est perforé et la couche infratectale columellaire (ex. *Hiraea cuneata*) chez les pollens porés. Les pollens des fleurs cléistogames (Fig. 1.22) ont comme dans le cas précédent, une exine immature dont le développement paraît stoppé lorsque la cellule est prête à germer.

En conclusion, comme dans les *Apterygiae,* les pollens colporés ont une couche infratectale columellaire et les pollens porés une couche granulo-columellaire ou grenue.

Genres de l'Ancien Monde

Seules trois tribus des Pterygophorae *sont représentées*

(a) *Rhynchophorae*

Le pollen sphérique est inaperturé, l'exine est verruqueuse et la couche infratectale columellaire, la nexine est endosculptée (Fig. 1.11).

(b) Banisterieae

(i) *Sphedamnocarpinae.* Le pollen subsphérique est colporé (*Brachylophon,* Asie) ou syncolporé (*Acridocarpus,* Fig. 1.13, *Rhynopterys,* Fig. 1.12, Afrique, Madagascar, Asie). L'exine est mince, réticulée, la couche infratectale columellaire (Fig. 1.24) et la sole moins épaisse que l'endexine.

Le pollen est poré, subsphérique (Fig. 1.17), parfois anguleux *(Ryssopterys)* et l'exine est verruqueuse, tectée, largement perforée ou gemmulée. La couche infratectale est columellaire, la sole peu épaisse et l'endexine très importante.

(ii) *Banisteriinae.* Il y a deux espèces localement représentées dans l'Ouest africain, *Brachypterys ovata* et *Heteropterys leona,* avec un pollen cubique poré à sillons vestigiaux, tectum perforé, couche infratectale columellaire, nexine réduite à l'endexine. Ce pollen est identique à celui des autres espèces de la tribu en Amérique.

(c) Hiraeeae

(i) *Aspidopteryginae.* Les pollen sont porés avec 4 (*Tristellateia,* Fig. 1.21), 6 (ex. *Triaspis,* Fig. 1.16), ou 6 à 12 pores inégaux (*Hiptage,* Fig. 1.20); les grains sont généralement subsphériques, anguleux, parfois cubiques (Lobreau-Callen, 1967, 1975); l'exine est plus épaisse aux angles des volumes, là où il existe des sillons vestigiaux, dans les genres Américains. Cet épaississement est dû à la couche infratectale columellaire plus haute, avec les milieux des columelles soudés *(Caucanthus),* ou grenue décollée de la nexine *(Hiptage).*

Lorsque l'exine est ornementée (ex. *Microsteira*), le tectum discontinu (ex. *Aspidopterys*), perforé (ex. *Flabellaria, Triaspis*), la couche infratectale est columellaire, la sole moins épaisse que l'endexine. Lorsque le tectum est lisse, rarement perforé, la couche infratectale est grenue (Fig. 1.29)

(ii) *Mascagniinae:* un seul genre *Digoniopterys.* Le pollen inaperturé présente les mêmes caractères que celui de *Rhynchophora.*

Chez les *Pterygophorae* de l'Ancien monde, les variations de structure de l'exine sont identiques à celles de toutes les Malpighiaceae du Nouveau Monde.

En conclusion, dans l'ensemble de la famille des Malpighiaceae, le pollen présente des caractères liés: les pollens colporés ont une couche infratectale toujours columellaire. Les pollens porés avec ou sans sillons vestigiaux ont une couche infratectale grenue ou columellaire. Chez ces pollens porés, lorsque l'exine est réticulée ou tectée avec un tectum largement perforé ou réticulé, donc discontinu, la couche infratectale est columellaire. Lorsque l'exine n'est pas ou à peine ornementée, le tectum étant continu, non perforé, lisse ou microstrié, la couche infratectale est grenue.

Dans l'ancien monde, le pollen des Malpighiaceae est celui qui est le mieux ornementé (tectum discontinu) avec une couche infratectale généralement columellaire, un seul genre ayant un tectum continu et une couche infratectale grenue: *Tristellateia.*

Chez les Malpighiaceae, les pollens porés avec ou sans sillons vestigiaux, à structure infratectale grenue, ont une nexine très épaisse, réduite presque essentiellement à l'endexine. Chez les pollens porés, columellaires, le sole est présente, continue et peu épaisse par rapport à l'endexine.

Les caractères de structure de l'exine sont ceux de nombreuses Polygalales, telles que les *Krameriaceae* (Larson & *al.,* 1962; Larson, 1964; Simpson & Skvarla, 1981). Elle est également comparable à celle des Légumineuses (Ferguson & Skvarla, 1981) et des Rutales (Horner & Lersten, 1971; Lobreau-Callen & *al.,* 1978).

En 1935, Wodehouse signale des sillons vestigiaux dans une famille autre que celle des Malpighiaceae, celle des Mimosaceae. Ce sont ces structures que Guinet appelle 'faux sillons' dans cette dernière famille. Chez les Malpighiaceae, la structure des sillons vestigiaux est celle de véritables sillons par la membrane aperturale due au tectum finement verruqueux et par l'absence de la couche infratectale; mais l'endexine n'étant pas modifiée, ces sillons ne jouent aucun rôle harmomégatique (Fig. 2.8 & 2.9). Ces sillons sont donc différents des "faux sillons" des Mimosaceae qui correspondent à une interruption du tectum (Guinet & Lugardon, 1976; Guinet, 1981).

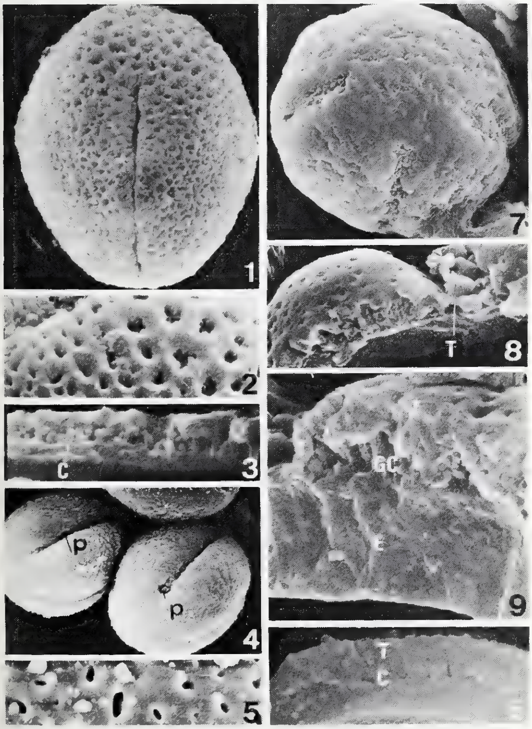

FIG. 2.— 1–3, *Galphimia brasiliensis* Juss. subsp. *australis* Chodat f. *australis* McBryde: 1, apertures complexes, × 2 000; 2, réseau avec le mur en forme de toît, terminé par une crête, × 5 000; 3, couche infratectale columellaire. 4–6, *Banisteriopsis nitrosiodora* (Griseb.) O'Don & Lourt.: 4, endoaperture (p) avec une disposition variable selon les apertures, × 500; 5, tectum perforé, × 5 000; 6, fracture de l'exine, columelles très courtes, × 5 000. 7–9, *Dicella bracteosa* (Juss.) Griseb.: 7, vue polaire, tectum finement perforé, × 1 100; 8, fracture d'exine au niveau d'un sillon vestigial, membrane aperturale verruqueuse, tectum perforé, couche infratectale granulo-columellaire, × 3 000; 9, détail de l'exine vers un sillon vestigial, membrane aperturale due au tectum, × 8 000. (C = columelle; E = endexine; G = grains; T = tectum.)

Par les variations de structure de l'exine, les Malpighiaceae (Polygalales pourraient être rapprochées des Légumineuses (Rosales) et des Rutales. Ces résultats étayeraient ceux de Dahlgren (1980), les sillons vestigiaux étant un caractère original. Par contre, la spiralisation des endoapertures n'a jamais été observée chez les Légumineuses, ni chez les Rosidae.

En 1960, Emberger rapprochait les Malpighiaceae des Malvales. Dans cet ordre, la spiralisation des apertures est remarquable, mais contrairement à ce qui est observé chez les Malpighiaceae, où seules les endoapertures sont disposées en spirales, la spiralisation affecte l'ensemble des apertures (ectoaperture + endoaperture). Nous pensons donc pour notre part que par le pollen, les ressemblances avec les Malvales ne sont que convergences. Chez les Euphorbiales, la spiralisation des apertures n'affecte que les endoapertures. Il existe donc des rapports palynologiques entre les Malpighiaceae et les Euphorbiaceae; en outre, ces deux familles présentent également des glandes nectarifères extraflorales.

RAPPORTS ENTRE LES POLLENS DES MALPIGHIACEAE DE L'ANCIEN MONDE ET CEUX DU NOUVEAU MONDE

Les pollens colporés de *Brachylophon* ou syncolporés de *Rhinopterys* et d'*Acridocarpus* sont comparables à ceux de la sous-tribu des *Galphimiinae (Galphimieae)* dans les *Apterygiae.*

Les pollens porés tétraédriques, réticulés ou tectés, largement perforés de *Flabellariopsis (Sphedamnocarpinae)* rappellent ceux de *Thryallis (Galphimieae,* sous tribu *Thryallidinae).* Ceux de *Tristellateia* ne se rapprochent de ceux de *Thryallis* que par la symétrie, la forme et la nexine aussi épaisse. Ils s'en distinguent par le tectum lisse reposant sur une couche grenue souvent localement décollée de la nexine.

Les grains hexaporés, columellaires d'*Aspidopterys, Calyptostylis, Flabellaria, Microsteira, Philgamia, Sphedamnocarpus* (espèces malgaches), *Triaspis* sont proches de ceux columellaires de *Bunchosia* dans les *Malpighieae* et de *Thryallis* dans les *Galphimieae,* bien que le nombre de pores ne soit pas le même.

Chez quelques genres africains, tels que *Flabellaria* et *Tristellateia,* le pollen peut présenter occasionnellement des sillons vestigiaux comme c'est le cas chez *Dicella, Thryallis* . . . c'est à dire les deux sous tribus des *Thryallidinae* et des

Malpighiinae à pollen poré avec ou sans sillons vestigiaux des *Apterygiae.*

Dans les trois genres *Caucanthus, Rhyssopterys* et *Hiptage* les types polliniques anguleux présentent quelques caractères communs: sexine épaissie au niveau des arêtes, brusquement interrompue au niveau des apertures, donnant ainsi à l'ectoaperture l'aspect d'un sillon vestigial transversal aux arêtes. De plus ces épaississements de la sexine ont la même disposition que les sillons vestigiaux des genres américains de la même sous-famille. Ce type pollinique n'existe que dans l'Ancien Monde.

Les pollens avec 12 à 24 pores des espèces africaines de *Sphedamnocarpus* et inaperturés de quelques genres malgaches ne trouvent pas d'équivalents en Amérique et en Asie.

En conclusion, les pollens de l'Ancien monde se rapprochent morphologiquement de ceux des *Apterygieae* en Amérique du Sud et ne présentent pratiquement pas de rapports avec ceux des *Pterygophorae* du Nouveau Monde. Seules les deux espèces ouest-africaines de la sous-tribu des *Banisteriinae* ont un pollen de type sud-américain.

ENCHAINEMENT DES DIVERS TYPES POLLINIQUES DES MALPHIGIACEAE

Les pollens tricolporés, réticulés, les plus petits avec le degré de symétrie le plus bas se trouvent dans les genres où les fleurs sont actinomorphes, ont un disque plan, où les fruits sont des capsules déhiscentes ou des drupes et où le nombre chromosomique de base est le plus petit.

Aux pollens hexacolporés ou syncolporés, microréticulés ou très largement réticulés, où les endoapertures sont disposées selon une spirale ou sont équatoriales, correspondent des fleurs légèrement zygomorphes, l'un des pétales étant plus grand, avec un disque plan *(Tricomaria),* parfois pyramidal *(Acridocarpus, Brachylophon, Dinemandra . . .),* des fruits samaroïdes ou tendant à l'être *(Tricomariae)* et un nombre chromosomique de base plus élevé.

Aux pollens porés avec des sillons vestigiaux, essentiellement chez les genres américains ou strictement ouest-africains, correspondent en général des fleurs nettement zygomorphes, avec un disque pyramidal, rarement plan *(Tricomariae,* sous-tribu des *Malpighiinae,* à l'exception de *Bunchosia);* les fruits sont des drupes ou des samares; les nombres chromosomiques de base sont élevés.

Les pollens porés sans sillons vestigiaux se rencontrent chez les genres de Madagascar, de l'Est africain, d'Asie, d'Océanie, rarement d'Amérique du Sud. En Asie comme en Océanie, les fleurs tendent à avoir un grand diamètre et à être zygomorphes, et, en particulier dans l'Ancien monde, le disque floral tend à être pyramidal et les fruits samaroïdes.

Si l'on admet que la fleur zygomorphe, le disque pyramidal, le fruit samaroïde à aile bien développée et souvent complexe sont des caractères dérivés, les pollens porés, avec ou sans sillons vestigiaux, de grand diamètre pouvant atteindre jusqu'à 70 µm de diamètre, un fort degré de symétrie *(Sphedamnocarpus* d'Afrique, *Brachypterys, Camarea . . .)* sont également dérivés.

Ainsi, il semble que chez les Malpighiaceae, l'aboutissement vers un pollen poré se soit réalisé selon deux grandes voies parallèles:

(1) à partir d'un pollen tricolporé, réticulé *(Galphimiinae),* vers un pollen où les apertures complexes tendent à être simples par transformation de l'ectoaperture qui s'élargit, s'ornemente et prend l'aspect de sillons vestigiaux qui tendent à se ramifier (*Galphimiinae: Lophanthera, Spachea):* il s'agit enfin de véritables sillons vestigiaux dont les ramifications se soudent; les sillons finissent par devenir particulièrement longs et étroits *(Malpighia)* et enfin disparaissent *(Bunchosia).* Simultanément, les endoapertures plus nombreuses passent de subéquatoriales: *Lasiocarpus, Psilochaeta, Dinemandra (Pterygophorae),* éventuellement disposées sur une spirale *(Dicella, Apterygiae; Echinopetrys, Pterygophorae),* à une répartition sur deux plans parallèles de part et d'autre de l'équateur (ex. *Malpighia, Bunchosia . . .*).

Correspondent à ce schéma les *Apterygiae,* sous-tribu *Malpighieae,* et les *Pterygophorae* américaines.

(2) à partir d'un pollen tricolporé, réticulé *(Galphimiinae),* vers un pollen poré par réduction *(Malpighieae p.p.)* ou transformation en apertures vestigiales (ex. *Galphimiinae: Clonodia, Heladena*), puis par perte des ectoapertures, augmentation du nombre des endoapertures disposées sur une spirale subéquatoriale *(Heladena),* puis sur deux plans *(Thryallis)* et enfin sur tout le pollen *(Sphedamnocarpus).* C'est le cas des *Apterygiae (Galphimiinae)* et des *Pterygophorae* de l'Ancien Monde.

Pour l'ensemble de la famille, il y a donc tendance à une simplification des apertures.

Ainsi, par la morphologie du pollen, les *Pterygophorae* dérivent des *Apterygiae* et plus particulièrement des *Galphimiinae.* Parmi les *Pterygophorae,* ce sont les *Tricomariae* qui ont les caractères polliniques les plus primitifs, ce qui est confirmé par les caractères floraux (Arènes, 1956). Les *Banisteriae* et les *Hiraeea,* difficilement distinctes apparaissent au même niveau évolutif et présentent toutes deux quelques grains relativement primitifs (colporés).

Dans l'ensemble des Malpighiaceae, accompagnant ces caractères, l'exine réticulée et la couche infratectale columellaire des grains les plus primitifs, devient lisse après s'être compliquée, le tectum repose sur une couche grenue chez les grains à sillons vestigiaux les plus hautement différenciés. La sole disparaît et l'endexine devient très épaisse et endosculptée (perforée et rugulée).

En conclusion, les pollens des Malpighiaceae les plus primitifs sont sud-américains; la souche de la famille se trouve donc sur ce continent.

Les pollens des *Pterygophorae* de l'Ancien Monde sont ceux dont la simplification des apertures est la plus poussée, ce qui laisse penser que leur histoire est ancienne; leur structure infratectale généralement columellaire les rapprochant des grains les plus primitifs, montre qu'ils sont issus des Malpighiaceae sud-américaines. Leur dispersion s'est donc faite nécessairement avant la séparation entre l'Afrique et l'Amérique. L'histoire des Malpighiaceae de l'Ancien Monde est donc antérieure à la fin du Crétacé supérieur. En outre, les pollens avec une structure infratectale grenue et un tectum continu étant principalement asiatiques, la spéciation la plus grande étant afro-malgache, il apparaît donc que l'Afrique et Madagascar sont les deux continents qui ont été colonisés les premiers. De plus, c'est à Madagascar que l'on rencontre les pollens les plus originaux (inaperturie), d'ailleurs chez des taxons endémiques. Madagascar a donc joué un rôle important de conservatoire et de centre de survie pour de nombreux genres (Dejardin, Guillaumet & Mangenot, 1973; Leroy, 1978) et l'isolement de l'île aura entraîné différents genres à évoluer indépendamment.

Les *Pterygophorae* sud-américaines ont généralement un pollen avec des sillons vestigiaux et donc n'ont pas acquis la simplification maximale des apertures, mais la structure de l'exine est hautement dérivée. Dans l'Ouest africain, les deux seuls représentants de ce groupe ont une exine columellaire donc plus proche de celle des types primitifs. Il apparaît donc que les *Pterygophorae* sud-américaines ont été mises en place au moment de la dérive des continents alors que des communications entre l'Afrique de l'Ouest et l'Amérique étaient encore possibles. Mais leur plus grande différentiation s'est faite durant tout le Tertiaire.

RAPPORTS ENTRE LES CARACTÈRES DU POLLEN ET CEUX DES GLANDES CALICINALES

La plupart des fleurs de Malpighiaceae ont des glandes calicinales de natures diverses. Il s'agit: de nectaires chez les genres de l'Ancien Monde et chez plusieurs *Apterygiae,* et d'élaiophores ou glandes à huile dans les genres du Nouveau Monde des *Pterygophorae,* parfois des *Apterygiae (Byrsonima p.p., Lophanthera, Malpighia, Bunchosia).*

Dans quelques genres et espèces de l'Ancien Monde (ex. *Sphedamnocarpinae p.p.*), des *Apterigiae* (ex. *Galphiminae* p.p.), le calice est totalement églanduleux et des *Tricomariae p.p.* dans les *Pterygophorae.* Les glandes sont nectarifères ou absentes dans les fleurs où le pollen est primitif ou poré et elles secrètent de l'huile dans les genres à pollens dérivés de l'Amérique du Sud.

RÉPARTITION DES CARACTÈRES POLLINIQUES DES MALPIGHIACEAE CLASSÉES SELON LES DONNÉES DÉ ANDERSON (1978)

Révisant actuellement la systématique des Malpighiaceae, Anderson propose de réduire la sous famille strictement américaine aux seuls genres à fruits vraiment dépourvus d'aile et à pollen colporé. Selon nos observations cette sous-famille des *Byrsonimoideae* serait ainsi réduite aux genres pour la plupart les plus primitifs de la famille où l'exine pollinique est la plus simple: réseau ou tectum largement perforé, couche infratectale columellaire, sole et endexine; le sillon est plus ou moins développé, ce dernier étant parfois intermédiaire entre les sillons fonctionnels bien délimités à membrane finement granuleuse et les sillons vestigiaux mal délimités à membrane fortement granuleuse voire même verruqueuse. C'est dans ce groupe que se situent les genres dont le type floral est le plus primitif en particulier par l'absence de glandes calicinales *(Galphimia* sect. *Microgalphimia).* Dans cette sous-famille, lorsqu'il y tendance à la parasyncolpie ou à la réduction des sillons qui deviennent vestigiaux, ou encore réduction des perforations tectales il y a acquisition de glandes calicinales ou transformation de glandes nectarifères.

Par contre tous les genres à fruits de structure dérivée de fruits ailés, ont un pollen poré. Selon nos résultats, il s'agit des genres à pollens avec ou sans sillons vestigiaux avec une structure exinique dérivée: tectum mince reposant sur une couche infratectale grenue, perte de la sole, endexine massive. Les affinités de ces genres sont plus précises avec les *Gaudichaudioideae (Pterygophorae)* pour Anderson; elle le sont également par les caractères du pollen.

Ainsi, dans tous les cas, quelque soit la classification choisie nos résultats palynologiques restent également valables et nous retrouvons toujours la dualité évolutive des apertures avec soit perte des ectoapertures, le pollen devenant poré, soit développement de l'ectoaperture (Lobreau, 1966, 1967; Lowrie in Anderson & Gates, 1981, pour les Byrsonimoideae seulement) qui plus tard devient vestigiale et finit par disparaître, le pollen étant alors poré. Ce même type de dualité existe pour les variations de structure de l'exine qui voit sa couche infratectale columellaire devenir soit granulo-columellaire puis grenue, soit columellaire avec des columelles plus hautes et complexes, plus ou moins anastomosées, pour enfin être remplacées par une structure grenue.

RELATIONS ENTRE L'ÉVOLUTION MORPHOLOGIQUE DU POLLEN DES MALPIGHIACEAE ET LES INSECTES POLLINISATEURS (SCHÉMA 1)

En 1974, Vogel faisait de nombreuses observations sur la pollinisation des Malpighiaceae néotropicales notamment. Plus récemment Buchmann & Hurley (1978) publiaient leurs résultats sur la pollinisation des plantes à étamines à déhiscence poricide (dont certaines Malpighiaceae font parties) et tout récemment Anderson (1979) donnait une interprétation des variations structurales de la fleur des Malpighiaceae en liaison avec la pollinisation par les insectes vibrants. Selon ce dernier auteur, les Malpighiaceae paléotropicales toutes dépourvues d' élaiophores calicinaux dérivent des Malpighiaceae néotropicales à calice à élaiophore et ont perdu leurs glandes calicinales à huile, les insectes pollinisateurs étant absents de l'Ancien monde. Par contre, en rapport avec cette réduction des élaiophores chez *Acridocarpus, Rhynopterys* et une espèce de *Tristellateia,* au cours de l'évolution il y aurait eu apparition d'étamines à déhiscence poricide attirant les insectes vibrants. Une adaptation comparable se retrouverait avec le genre néotropical *Coleostachys.*

Les Malpighiaceae sont pollinisées par les Hyménoptères. Vogel (1974) a remarqué qué en Amérique du Sud, la pollinisation est assurée uniquement par certains genres d'*Apoidea* et plus particulièrement par quatre genres d'*Anthophorinae, Apidae* primitifs qui nichent presque tous dans la terre; il s'agit des femelles de *Tetrapedia, Paratetrapedia, Epicharis* et *Centris* qui recherchent les huiles végétales indispensables (?) à la nutrition des larves. Plusieurs *Malpighiaceae* sont également fécondées par d'autres *Apides* tels que des *Apidae* primitifs *(Euglossinae)* ou évolués *(Meliponae)* ainsi que par une abeille ou *Apiodea* inférieur des *Halictidae (Halictus).*

A Java, comme dans toute l'Asie, le genre *Hiptage* est pollinisé par *Xylocopa* qui est également un *Apidae* primitif, mais de très grande taille (30 mm); adapté à la pollinisation des fleurs zygomorphes.

En Amérique du Sud, chez les genres à fleurs zygomorphes avec des glandes calicinales très développées et à gros pollens à sillons vestigiaux (tels que *Tricomaria usilo,* dont les fleurs sont fécondées par *Centris brethesii, Heteropterys sp.* pollinisé par *Tetrapedia, Stigmatophyllum* sp. par *Centris* ou par *Epicharis* selon les espèces) il y a adaptation à la pollinisation par les *Anthophorinae,* insectes ayant une langue longue. Chez *Centris,* genre le plus évolué, les pattes sont particulièrement modifiées facilitant ainsi la récolte de l'huile végétale et du pollen; c'est en outre dans les taxons botaniques où la pollinisation est assurée par l'*Anthophorinae* le plus évolué que le pollen est le plus différencié avec la structure exinique la plus modifiée (tectum lisse, couche infratectale grenue, absence de sole).

Par contre, chez les genres à fleurs actinomorphes ou faiblement zygomorphes à glandes calicinales peu développées ou absentes, à pollens moins gros, voire même de petites dimensions (ex. *Apterygiae p.p.*), les Hymémoptères pollinisateurs sont beaucoup plus nombreux et appartiennent à diverses familles des *Apoidea:* aux *Apoidea* inférieurs *(Halictus)* avec une langue relativement courte, ou supérieurs avec la famille des *Apidae.* Il s'agit d'*Apidae* primitifs (*Anthophorinae, Euglossinae* chez lesquels la langue est très développée et la brosse à cire rudimentaire, mais adaptés à la récolte de l'huile des fleurs) ou plus rarement d'*Apidae* évolués tels que les *Meliponae* et les *Apinae* qui fabriquent de la cire, mais ne sont généralement pas adaptés à la récolte de l'huile (une exception peut être avec *Trigona*).

Les taxons botaniques pollinisés par toute sorte d'insectes ont des fleurs actinomorphes à calice généralement dépourvu d'élaiophores et un pollen colporé, réticulé (ex. *Galphimia*); ceux pollinisés par les *Anthophorinae* et tout particulièrement par les trois genres les moins évolués ont des fleurs encore actinomorphes ou faiblement zygomorphes, un calice présentant des élaiophores et un pollen colporé ou poré généralement avec des sillons vestigiaux. Dans tous les cas, le pollen est généralement ornementé avec une ectexine à tectum perforé, une couche infratectale columellaire, une sole plus ou moins réduite. Lorsqu'il y a apparition de la zygomorphie et des élaiophores, simplification des apertures du pollen, il y a coadaptation à la pollinisation par les *Anthophorinae.*

Ainsi, en Amérique du Sud, alors qu'il y a évolution des types floraux vers la zygomorphie, apparition des glandes à huile qui deviennent de plus en plus importantes et complexes (anastomoses), augmentation du volume du pollen dont la structure ectexinique tend à devenir homogène (tectum continu lisse, reposant sur des grains de sporopollenine), il y a adaptation et spécialisation de quatre genres puis d'un seul genre d'*Anthophorinae,* morphologiquement adaptés pour la récolte de l'huile et du pollen. Il y a donc coadaptation et coévolution.

Les quatre genres d'*Anthophorinae,* comme les Malpighiaceae à glandes calicinales à huile sont également strictement sud-américains. Cette coadaptation a donc eu lieu alors que des échanges avec les autres continents et tout particulièrement entre l'Amérique du Sud et le bloc afro-asiatique n'étaient plus possibles, donc durant le Tertiaire. Cette évolution est par conséquent récente. Toutefois, la présence de quelques représentants des Malpighiaceae à pollens avec des sillons vestigiaux de type américain dans l'Ouest-africain tendait à montrer que l'évolution de ces Malpighiaceae se serait faite très tôt alors que quelques échanges étaient encore réalisables entre les deux continents; mais le type pollinique peu évolué dans sa sous-tribu et la faible dispersion des genres montre que ces espèces ont été mises en place en Afrique, dans l'Ouest-africain, antérieurement au développement de ces quatre genres d'insectes absents de l'Ancien Monde. D'ailleurs ces *Anthophorinae* se seraient différenciés avant la fin du Crétacé supérieur, alors que les premiers Hyménoptères existaient déjà depuis la fin de Jurassique avec le groupe des Symphytes, Hyménoptères les plus archaïques (pollinisateurs ?).

Les Malpighiaceae de l'Ancien Monde dont l'histoire est antérieure à la fin du Crétacé supérieur sont affines des genres américains dont la pollinisation est assurée par les *Apoidea* variés *Anthophorinae, Euglossinae, Halictidae, Xylocopinae, Meliponae).* Or ces Malpighiaceae, principalement les *Galphimiae,* présentent ou non des glandes calicinales généralement nectarifères, plus ou moins développées selon les espèces, comme chez les *Pterygophorae* de l'Ancien Monde, où la pollinisation est effectuée par divers Hyménoptères.

Les glandes nectarifères attirent des insectes variés. Chez les genres dépourvus de glandes à huile, le pollen a généralement de relativement petites dimensions et est particulièrement abondant car il est souvent consommé par les insectes attirés par le nectar.

En Afrique et à Madagascar, les groupes des *Apoidea* connus pour polliniser les fleurs des *Apterygiae* en Amérique, sont tous représentés et très largement diversifiés avec de nombreuses espèces endémiques (De Saussure, 1891; Benoist, 1962). Il faut citer tout particulièrement le genre *Trigona* dans les *Meliponae,* issu d'Amérique du Sud et connu comme agent fécondant des Malpighiaceae primitives américaines; le genre *Xylocopa* particulièrement attiré par les fleurs zygomorphes, connu dans tout l'Ancien Monde et observé à Java sur des fleurs d'*Aspidopterys.* A Madagascar et en Afrique, d'autres genres de *Xylocopinae* peuvent également intervenir, en particulier le genre *Allodape* dont le corps a de petites dimensions, 2 ou 3 mm. D'autre part, l'*Halidictidae* primitif, *Nomia* et le genre *Halictus* déjà connu comme agent fécondant de fleurs de Malpighiaceae en Amérique du Sud, sont particulièrement abondants à Madagascar, notamment dans les régions où l'on trouve les trois genres endémiques *Rhynchophora, Calyptostylis* et *Digoniopterys.*

Chez les genres de l'Ancien Monde, le pollen beaucoup moins gros que celui des genres américains est agglutiné ou non par le nectar et les Apides peuvent ainsi aisément collecter le pollen grâce à leurs pattes plus ou moins modifiées pourvues d'une brosse. Il n'y a donc pas dans l'Ancien Monde, cette coadaptation observée en Amérique du Sud entre les caractères gros pollen-abondantes sécrétions huileuses- insectes adaptés aux récoltes de ces produits.

Chez les Malpighiaceae de l'Ancien Monde comme chez les *Galphimiae* du Nouveau Monde, lorsque les anthères ont une déhiscence poricide, il y a coadaptation à la pollinisation par de gros Apides qui font de nombreuses vibrations avec leurs ailes provoquant ainsi l'expulsion du pollen des anthères, pollen qui a toujours de petites dimensions, colporé et dont les ectoapertures modifiées (une exception *Coleostachys*) sont soudées (syncolpie ou parasyncolpie) ou absente dans le cas de *Tristellateia* et où les mailles du réseau tendent à disparaître. Cette forme de coadaptation à divers insectes est la seule qui existe chez les Malpighiaceae de l'Ancien Monde. Du fait de son existance également dans le Nouveau Monde il semble que l'on puisse affirmer que ce type de coadaptation apparue antérieurement au Crétacé supérieur soit la première connue.

Les pollens des *Pterygophorae* américaines tendent à devenir tectés, lisses et à remplacer la structure infratectale columellaire par une structure grenue. Cette remarque est particulièrement nette chez les genres où il y a adaptation à la pollinisation par des insectes définis. Mais cette modification de structure exinique existant dans l'Ancien Monde, il n'est pas possible de dire que l'adaptation entraîne une modification de structure exinique. Il semble toutefois qu'elle l'accentue. Cette observation confirme celle que nous avions déjà faite chez les Santalales (Lobreau-Callen, 1980).

Le peuplement de l'Ancien Monde en Malpighiaceae est donc antérieur au Tertiaire, à une époque où les *Apoidea* se différenciaient. En outre, toutes les espèces de Malpighiaceae, à quelques très rares exceptions près, présentent des glandes à nectar calicinales ou au moins sur l'appareil végétatif et sur les inflorescences. Ces glandes sont régulièrement visitées par de nombreux insectes tels que les fourmis, les guêpes, et même parfois certains Lépidoptères *(Sphingidae).* Or les fourmis sont connues depuis le Crétacé et les guêpes depuis le Jurassique supérieur. Si les fourmis ne paraissent pas être actuellement des insectes pollinisateurs, il semble que l'on ne puisse pas être aussi affirmatif avec les guêpes; or ces insectes sont également très abondants dans l'Ancien Monde.

En conclusion, en choisissant l'exemple des Malpighiaceae, nous avons pu montrer qu'il y avait eu en Amérique du Sud coadaptation et coévolution (Fig. 3): Insectes pollinisateurs — Augmentation du nombre chromosomique de base — Développement des glandes à huile — Accroissement en dimensions et en nombre d'apertures du pollen, relativement

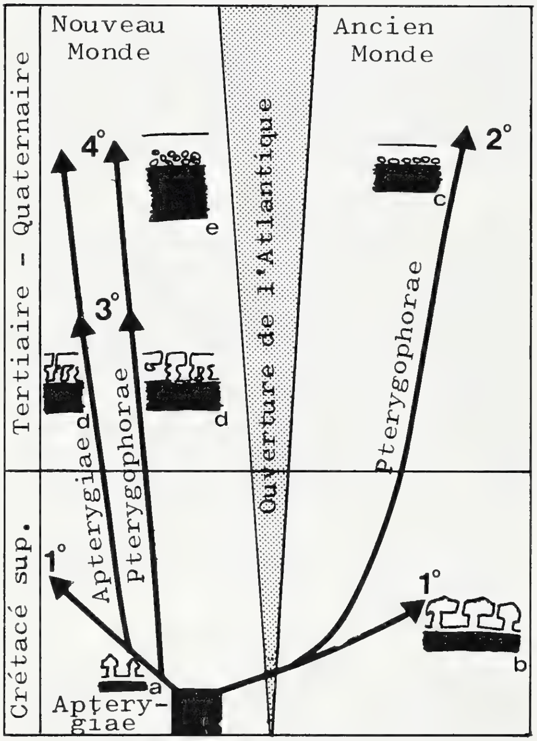

FIG.3.—La coévolution insectes pollinisateurs — types polliniques chez les Malpighiaceae: 1°, Adaptation à la pollinisation par de gros insectes de différents groupes d'Apides qui font expulser le pollen des anthères par leurs vibrations: structure columellaire de l'exine; 2°, Adaptation à la pollinisation par divers insectes qui recherchent les fleurs zygomorphes: structure grenue de l'exine; 3°, Adaptation à la pollinisation par un groupe d'insectes qui recherchent des substances sécrétées par les fleurs et indispensables à leur survie: structure granulo-columellaire de l'exine; 4°, Adaptation à la pollinisation par un genre précis d'insectes hautement différenciés: structure grenue de l'exine.

Lorsqu'il n'y a pas coadaptation, le pollen est réticulé et les columelles sont hautes.

Exemples de structure de l'exine: a, *Galphimia brasiliensis;* b, *Echinopterys eglandulosa* pour le Nouveau Monde ou *Acridocarpus humbertii* pour l'Ancien Monde; c, *Hiptage madablota;* d, *Bunchosia* sp. pour les *Apterygiae, Peixotoa jussieuana* ou *Banisteriopsis nitrosiodora* pour les *Pterygophorae;* e, *Malpighia glabra* pour les *Apterygiae* ou *Tricomaria usilo* pour les *Pterygophorae.* (Sont figurés en blanc, l'ectexine et en noir l'endexine.)

récemment durant le Tertiaire, à partir de Malpighiaceae déjà différenciées depuis le Crétacé et avec des fleurs à calice généralement dépourvu de glandes nectarifères. Par contre, dans l'Ancien Monde et en particulier en Afrique et à Madagascar, où les séries évolutives ont été mises en place antérieurement au Tertiaire à partir de l'Amérique du Sud, il n'y a pas eu coadaptation; on ne connaît pas d'hyménoptères particulièrement adaptés aux fleurs de Malpighiaceae; il n'y a pas eu développement particulier des glandes à huile et le pollen ne présente généralement pas de trés grandes dimensions. Mais l'isolement particulièrement ancien des Malpighiaceae en Afrique et à Madagascar a favorisé l'évolution des genres de manière originale, ce qui explique le formidable endémisme observé au sein de la famille.

Ainsi, dans les Malpighiaceae, la coadaptation ayant eu pour conséquence l'importante évolution des types polliniques à sillons vestigiaux et l'acquisition de glandes à huiles est un caractère récent, secondairement apparu durant tout le Tertiaire, uniquement sur le continent américain isolé du reste du monde.

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Je tiens à remercier très vivement Monsieur le Professeur Leroy, Directeur du Laboratoire de Phanérogamie du Museum à Paris, Monsieur Brenan et Monsieur Green, Directeurs des Herbiers à Kew et Monsieur Kapp, Conservateur de l'Herbier de Strasbourg, qui ont mis ce matériel d'étude des Malpighiaceae à notre disposition.

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Les observations en microscopie électronique ont été réalisées grâce à l'obligeance de Messieurs les Professeurs Lehman et Leclaire.

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LISTE DES ÉCHANTILLONS ILLUSTRÉS

Acridocarpus humbertii J.Ar.: Madagascar, Vallée Onilahy, *Capuron* 27 906 SF.

Aspicarpa hartwegiana A. Juss.: Paraguay, *Pringle* 697 P.

Aspicarpa linearifolia (St. Hil.) Ndz: Paraguay, *Hassler* 4581 K.

Banisteriopsis nitrosiodora (Griseb.) O'Don. & Lourt.: Bolivie, *d'Orbigny* 700 P.

Banisteriopsis elegans (Tr. & Pl.) Sander subsp. *cordata* (Ndz) Sander var. *pulcherrima* Sander: Guyane britannique, *Whitton* 206 K.

Bunchosia media DC.: Amérique, *Duchassaisaing* 1855 Str.

Byrsonima sp.: Trinidad, *Philcox, Wood & Kalloo* 7431 P.

Dicella bracteosa (Juss.) Griseb.: Brésil, Santa Catharina, *Klein & Souza* 6470 P.

Echinopterys eglandulosa (Juss.) Small: Mexique, *Diguet* s.n.P.

Galphimia brasiliensis Juss. subsp. *australis* Chodat f. *australis McBryde:* Brésil, Minas Geraes, *Saint Hilaire* 928 C° P.

Gaudichaudia cynanchioides H.B.K.: Mexique, *Arsène* 1950 P.

Heladena bunchosioides (A. Juss.) A. Juss.: Paraguay, *Balansa* 2403 P.

Hiptage madablota Gaertner: Indochine, *Eberhardt* 47110 P, Inde, Mohand Sanctuary, *Rao,* 38961 BSI (NC)

Lophanthera lactescens Duke: Brésil, Rio de Janeiro, *Duke* 23639 P.

Malpighia galeottiana A. Juss.: Cultivé à Friburg en 1856, P.

Peixotoa jussieuana Mast.: Brésil, *Blanchet* 1838 P.

Rhynchophora humbertii J. Ar.: Madagascar, *Humbert* 14225 P.

Rhynopterys kerstingii (Eng.) Ndz.: Gambie, *Berhaut* 4384 P.

Sphedamnocarpus angolensis (A. Juss.) Planch. ex Oliv.: Angola, *Bonnefoux & Villain* 67 P.

Tetrapterys citrifolia Pers.: Guyane française, *Mélinon* 336 P.

Triaspis hispida Pierre ex Badré: Gabon, *Klaine* 1228 P.

Tricomaria usilo Guill. ex Hook. & Arn.: Argentine, *Boecher, Hjerting, Rahn* 1077 P.

Tristellateia africana S. Moore: Kenya, Mombassa, *Sacleux* 834 P.

Bothalia 14, 3 & 4: 883–888 (1983)

Aspects of pollination and floral development in *Ficus capensis* Thunb. (Moraceae)

H. BAIJNATH* and S. RAMCHARUN*

ABSTRACT

A unique obligatory symbiosis exists between *Ficus capensis* Thunb., and its pollinator, *Ceratosolen capensis* Grandi. Flowers from both aerial and geocarpic syconia may be pollinated and produce seeds. Females of *C. capensis* possess specialized mesothoracic pockets in which pollen is transferred from ripening syconia to receptive ones. A second primary sycophile, *Sycophaga cyclostigma* Waterston, appears to be ineffective in pollination. Several secondary sycophiles oviposit through the syconial wall. Strong sexual dimorphism exists in most sycophilous wasps. All female flowers have the potential to produce either seeds or galls and variation is merely one of gross morphology. Flowering is distinctly asynchronous. Seeds are dispersed by various fruit predators and germinate very easily under warm humid conditions.

RÉSUMÉ

ASPECTS DE LA POLLINISATION ET DU DÉVELOPPEMENT FLORAL CHEZ FICUS CAPENSIS *THUNB. (MORACEAE)*

Une symbiose obligatoire unique existe entre Ficus capensis *Thunb. et son pollinisateur* Ceratosolen capensis *Grandi. Les fleurs des sycones tant aérien que géocarpiques peuvent être pollinisées et produire des graines. Les femelles du* C. capensis *possèdent des poches mésothoraciques spécialisées dans lesquelles le pollen est transféré des sycones en voie de maturation à ceux qui sont réceptifs. Un second insecte sycophile primaire,* Sycophaga cyclostigma *Waterston, semble être inefficace pour la pollinisation. Plusieurs sycophiles secondaires pondent au travers de la paroi du sycone. Un fort dimorphisme sexuel existe chez la plupart des guêpes sycophiles. Toutes les fleurs femelles ont la possibilité de produire soit des graines soit des galles et la variation concerne seulement la morphologie générale. La floraison est distinctement asynchrone. Les graines sont dispersées par divers animaux frugivores et elles germent très facilement sous des conditions humides et chaudes.*

INTRODUCTION

The Cape fig, *Ficus capensis* Thunb.**, has a fairly widespread distribution extending from the Eastern Cape through central Africa as far north as Ethiopia. It commonly occurs in damp areas along stream and river banks and in low-lying depressions. The tree is of moderate size reaching a height of 10–12 metres in the Durban area. *F. capensis* is a member of the sub-genus *Sycomorus* Gasp., and is especially interesting in that it bears both aerial and geocarpic figs (= syconia). A classic case of obligatory mutualism exists between members of the genus *Ficus* L., and small chalcid wasps of the family Agaonidae and several aspects of this study have been reviewed recently (Janzen, 1979). The fig tree is completely dependent on the wasps for pollination and seed production while the wasp completes its ontogeny within the syconium. Since the structure and life patterns of both mutualistic partners are so closely integrated to form a functional system, each pollinator is believed to be species-specific (Wiebes, 1964). The agaonid pollinator of *F. capensis* is *Ceratosolen capensis* Grandi.

MATERIALS AND METHODS

Most of the observations were carried out on an experimental tree located on the campus of the University of Durban-Westville. The developmental cycle of the syconium was monitored by daily measurements of 15 marked syconia. Different stages were gathered and studied in the laboratory. Insects were collected by placing mature syconia in erlenmeyer flasks sealed with muslin cloth. The wingless male wasps were removed by dissecting the syconia and washing in alcohol. Insect behaviour was determined by cutting open syconia and observing under a dissecting microscope. The fate of unpollinated syconia was studied by bagging very young syconia with fine nylon mesh. Conditions of foliage and flowering of 54 trees in and around the Durban area were recorded at 4–5 week intervals over a period of 13 months.

FLOWERING

1. *The fig flowers*

The small unisexual flowers of *Ficus capensis* are borne in hollow receptacles referred to as figs or syconia. These heart-shaped syconia occur on branched peduncles (Fig. 1A) arising from the trunk and aerial branches as well as from underground wood. Most of the inner surface of the receptacle is lined by female flowers, while relatively few (10–25), male flowers occur in 2 or 3 series around the descending ostiolar bracts. Each staminate flower is simple in structure consisting of 2 (rarely 3 or 4) large stamens enclosed by 3 to 4 perianth

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**Dr C. C. Berg of the Instituut voor Systematische Plantkunde, Rijksuniversiteit, Utrecht, Netherlands, has drawn our attention to the fact that *Ficus sur* Forssk. is an earlier published name for *F. capensis* Thunb. He has examined the types and is of the opinion that the two species are conspecific.

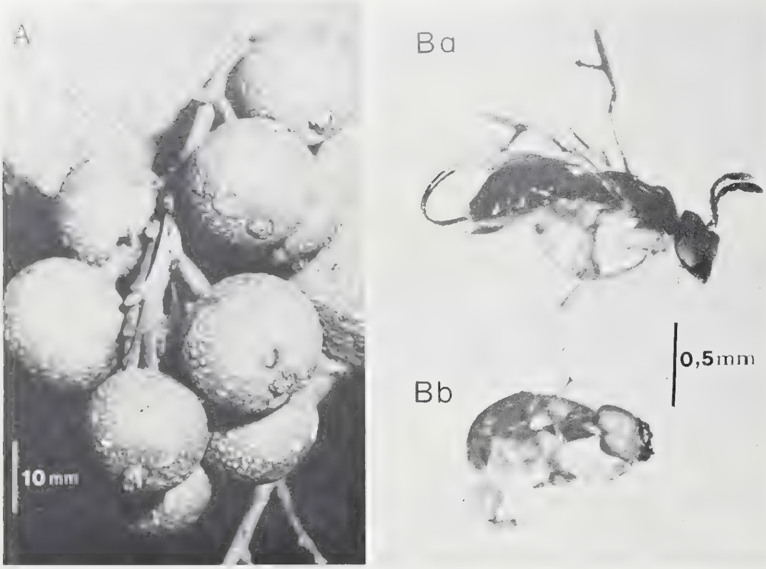

FIG. 1.—Some characters of syconia and pollinators in *Ficus capensis.* 1A, peduncle with several syconia; 1Ba, female and 1Bb, male of the regular pollinator, *Ceratosolen capensis.*

segments. At anthesis, which occurs several weeks after the female flowers are receptive, there is rapid elongation of the filaments so that the anthers protrude out of the perianth. The protogynous nature of syconial development thus effectively prevents selfing within the syconium.

Each female flower consists of a conspicuous ovary with a laterally attached style and 3 reduced perianth segments. The ovary is unilocular with a single large ovule attached laterally close to the stylar region. The flowers may be either sessile or borne on pedicels of varying lengths. Flowers with relatively elongate pedicels are short-styled and are functionally gall flowers. Sessile and short-pedicelled flowers have relatively long styles and are functionally seed flowers. This reciprocal staggering of style and pedicel lengths results in the overall height of all flowers being identical so that their stigmas form a continuous surface or synstigma lining the syconial cavity (Galil & Eisikowitch, 1968a). Each stigma is capitate with a characteristic central depression and short stigmatic papillae.

2. *The developmental cycle of the syconium* (Fig. 2)

The phenophase in *Ficus capensis* requires a period of about 60 days. The five phases of syconial development recognized by Galil & Eisikowitch (1968b) will be adopted in this description.

A or the prefloral phase: This is a period of 3 weeks from the initiation of the syconia until a diameter of approximately 1 cm is attained. The very young syconia are completely covered by tiny scales that are deciduous very early in the prefloral stage. Active growth and development of female flowers occurs during this period.

B or the female phase: The female flowers become receptive when the syconium is 22–24 days old. At this stage, the male flowers are immature and the stamens remain tightly enclosed within the perianth. The ostiolar bracts loosen slightly and females of the legitimate pollinator, *Ceratosolen capensis,* force their way into the syconium through the ostiole. Here they oviposit into short styled flowers and effect pollination of the long styled flowers by the removal of pollen grains from specialized mesothoracic pollen pockets. Usually about 1–3 wasps enter each syconium. These are often damaged as wings and antennal flagella are torn off as they force their way between the ostiolar bracts. In many instances dead wasps were found trapped between bracts. A second primary sycophile *Sycophaga cyclostigma* also enters the syconium during this time and oviposits into female flowers.

C or the interfloral phase: After pollination there is a long interfloral stage lasting approximately 30 days.

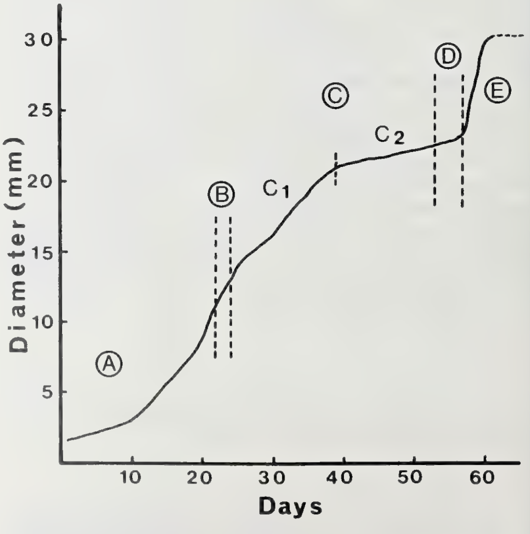

FIG. 2.—Growth curve of the syconium of *Ficus capensis* showing phases in the developmental cycle. A, prefloral; B, female; C, interfloral; D, male; E, postfloral.

During the first half of the interfloral phase (C_1) growth of the syconium continues at a more or less normal rate and is accompanied by rapid hardening of the syconial wall. During the latter half, C_2 growth slows down tremendously so that an increase in diameter of only 2 mm was recorded over a period of 15 days. During the interfloral stage the fig embryos develop in the seed flowers while the wasps pass through the larval and pupal stages in the gall flowers.

D or the male phase: The onset of the male phase, which lasts for 3–4 days, is indicated by a slight softening of the syconial wall. This is often accompanied by a very subtle change in colour from green to olive. The male flowers now attain maturity and the stamens protrude out of the perianth by rapid elongation of the filaments. At the same time the wasps reach the imago stage and the male wasps promptly bite their way out of their native galls. They then actively seek out galls containing female wasps, bite through the walls and fertilize the females within. They are also responsible for detaching anthers from the filaments, so that these become scattered within the syconium. When fertilization is complete, male wasps congregate at the ostiolar end and together bite a neat channel through the bracts to the outside. During this time the females release themselves from their galls by widening the opening made by the male wasps during fertilization. On eclosion, they actively fill up the mesothoracic pockets with pollen from the anthers and eventually leave the syconium through the channel prepared by the male wasps. The blind, wingless males are short-lived and die soon after preparation of the exit channel.

E or the postfloral phase: With the completion of the male phase there is a rapid increase in diameter of the syconium. The syconium wall becomes soft and succulent and changes to an attractive deep red colour with a sweet odour. The postfloral period may last for a maximum of 4 days at the end of which the syconia either fall to the ground or are eaten by various fruit predators.

3. *Unpollinated flowers*

Preliminary experiments were carried out to ascertain the fate of unpollinated flowers by bagging young pre-receptive syconia with a fine nylon mesh. At the receptive stage these syconia remained at a constant diameter for almost a week before abscissing. Infected figs of the same age, had during this week increased in diameter and thereafter continued normal development.

From field observations it was noted that figs infected by *Sycophaga cyclostigma* only, continued normal development but without the production of seeds. It is, therefore, apparent that the act of ovipositing stimulated parthenocarpic development of the syconia. This phenomenon is also reported for *Ficus sycomorus* L. infected by *Sycophaga sycomori* L. in the Middle East (Galil, Dulberger & Rosen, 1969). Such unpollinated syconia in *F. capensis* showed a high percentage of empty degenerate flowers.

4. *Asynchronous flowering*

Observation of 54 trees of *F. capensis* over a period of 13 months clearly indicates that the production of syconia is not seasonal. Trees bearing syconia of any developmental stage can be found during every month of the year (Table 1). However, flowering tends to increase slightly from December to April (Table 2). This co-incides with the warm, wet months of the year. Some trees displayed continuous fruiting throughout the year with little or no resting period between crops.

TABLE 1.—Percentage of trees displaying young, mature or ripe stages of syconial development during each month of the year*

Month	Young	Mature	Ripe
June 1980	26	59	15
July	35	70	24
August	22	61	22
September	51	71	23
October	37	70	46
November	37	65	48
December	41	74	39
January 1981	54	78	28
February	41	69	41
March	35	80	22
April	20	57	26
May	22	74	35
June	35	69	28

*For the purposes of this analysis — young = prefloral to female; mature = interfloral to male; ripe = postfloral.

Although each tree usually produces syconia in distinct crops, these may sometimes overlap to such an extent that young, mature and ripe syconia may occur simultaneously on an individual tree. In such instances, subsequent crops are initiated before the original crop has completed the developmental cycle. Furthermore, aerial and geocarpic crops may be initiated independently and may therefore be at different developmental stages at a particular time. The phenomenon of crop overlap (Table 3) and continuous fruiting occurred to a slightly greater extent during the summer period. Trees seem to vary in degree of deciduousness. Whereas some trees appear to be evergreen, others shed their leaves fairly regularly. Unlike the situation reported (Wharton, Tilson & Tilson, 1980) in *F. sycomorus*, no fixed correlation could be established between flowering and leaf drop in *F. capensis*.

5. *The symbionts of the syconium*

The living organisms associated with the syconium are many and include protozoans, yeast, fungi, nematodes, mites, beetle larvae, caterpillars and wasps. The syconium is therefore a very favourable microhabitat harbouring a variety of life forms. However, only the wasps are of direct significance in pollination and seed production. Most of the sycophilous wasps display elaborate sexual dimorphism. The females (Fig. 1 Ba) are active and winged with well developed sensory structures. The males (Fig. 1 Bb) are very much reduced in structure and are relatively pale coloured and wingless. They are often blind or may have vestigial eyes and reduced

TABLE 2.—Numbers of trees bearing syconia during each month of the year, expressed as a percentage of the sample

Month	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
%	67	82	72	82	87	80	90	96	91	91	90	87	83

TABLE 3.—Percentage of individual trees bearing young, mature and ripe syconia simultaneously (A). This phenomenon displayed on an exclusively aerial (A^1) or geocarpic (A^2) basis, is also recorded for each month

Month	A	A^1	A^2
June 1980	5,6	1,9	0
July	1,9	0	0
August	5,6	0	0
September	7,4	2,8	1,8
October	13,0	5,6	0
November	11,1	1,9	3,7
December	14,8	9,3	3,7
January 1981	9,3	7,4	3,7
February	13,0	9,3	5,6
March	9,3	7,4	3,7
April	5,6	0	0
May	7,4	7,4	0
June	5,6	0	1,8

antennae. Their most striking feature is a pair of very large, scissor-like mandibles. According to Wiebes (pers. comm.), who has undertaken the identification, the following taxa are involved:

Ceratosolen capensis — Primary sycophile (legitimate pollinator)
Sycophaga cyclostigma — Primary sycophile
Apocrypta sp. — Secondary sycophile
Parakoebelea sp. — Secondary sycophile
Eukoebelea sp. — Secondary sycophile
Sycophila sp. — Secondary sycophile
Camarothorax sp. — Secondary sycophile
Sycoscapter sp. — Secondary sycophile

At least eight species of wasps have been recovered from mature syconia in the Durban area. Most of these are secondary sycophiles (parasites and inquilines) and oviposit through the walls of the syconia. The inquilines do not directly affect seed production since they develop in already induced galls. Females of *C. capensis* and *S. cyclostigma* enter the syconium through the ostiole during the female phase of development. Observations appear to indicate that the main activity period of the former precedes that of the latter by about a day. The entry of females of *S. cyclostigma* into the syconium has been observed on many occasions. Such syconia containing active females of *S. cyclostigma* usually contain dead or dying females of *C. capensis*.

On entry into the syconium the behaviour of these two primary sycophiles is very distinctive. The females of *C. capensis* move about on the synstigma with the posterior extremity of the abdomen curled downwards. The triangular flap which supports the protrusible ovipositor is held underneath the body in a position perpendicular to the synstigma. At this stage, the ovipositor is only slightly extended and the tip is then positioned into the depression of a stigma. The body vibrates slightly and within a few seconds the ovipositor is completely extended down the style. The tip of the triangular flap now comes to lie in the stigmatic depression. This provides additional support as the prothoracic legs are folded backwards until the distal segments are at the entrance of the mesothoracic pockets. Pollen is then unloaded by a series of 'shovelling' movements which may occur from 3–14 times. Thereafter, the legs are dusted against each other, the ovipositor is withdrawn and the insect moves onto another stigma. Sometimes the ovipositor is only partly inserted into the style and retracted almost immediately. During these trials no pollination movements occur and there is apparently no release of eggs.

The females of *S. cyclostigma* remain very straight and flattened against the synstigma and display no perceptible movement while ovipositing. However, unlike the females of *C. capensis*, they usually tend to withdraw their ovipositors on exposure to light. Thereafter, they appear to make constant attempts to 're-enter' the syconium by crawling through the bracts.

In male or D-phase syconia only the males of *C. capensis* are involved in anther cutting and preparation of an exit channel. On a few occasions ripe syconia without exit channels were dissected to reveal a mass of dead or dying insects. Such syconia were found to contain an exclusive population of *S. cyclostigma*. Aggressive behaviour amongst males (inter- and intra-specific) had been observed on several occasions especially within more crowded syconia.

On eclosion from their native galls, females of *S. cyclostigma* become involved in an elaborate cleansing ritual, commencing with the removal of an antennal moult. Grooming movements of females of *C. capensis* are chiefly restricted to smoothing out of the wings with the use of the pro- and metathoracic legs. There is no antennal moult. The sequence of pollen collecting has not been observed since females of *C. capensis* seek immediate escape on dissection of the syconium. However, females leaving the exit channel always have their mesothoracic pockets laden with pollen grains. Pollen collecting has been observed in some other species of *Ficus*.

6. *Fruit dispersal and seed germination*

The ripe syconia of *F. capensis* are extremely attractive, being deep red in colour and usually occurring in large clusters on elongated peduncles. The walls of the syconia are soft and succulent (water content averages 84,5%) and are favoured by several birds, fruit beetles and possibly bats and other arboreal mammals as a source of food. Seeds are dispersed in this manner. Several species of flies, moths, bugs and hymenopterans are also very active around ripening syconia.

A series of germination trials undertaken in growth cabinets indicated 100% germination in all cases. The most rapid germination and best overall growth was obtained under conditions of high temperature (30°C) and humidity (80%). Seeds subjected to conditions of low temperature (15°C) required several additional weeks for germination.

7. *Some interesting observations*

Normally very enlarged galls contain individuals of *Sycophila* sp. or *Camarothorax* sp. These thick walled galls usually occur in groups and, because of the great increase in size, their walls become angular as they coalesce. On a few occasions such enlarged galls were found to contain 5–9 females of *Apocrypta* sp. In another instance 13 females of *S. cyclostigma* emerged from such an enlarged gall. It is not known whether these developed from numerous eggs that were deposited into a single ovary or whether they were a result of polyembrony. However, a male and female wasp were also dissected out of a slightly enlarged ovary. Although these were embryonic, the female could be identified as belonging to the genus *Apocrypta*. The male could not be recognized with any certainty. The fact that these were of separate sexes indicates that they developed from separate ova.

A very unusual find on the experimental tree was the discovery of two 'seed syconia' (1 aerial and 1 geocarpic). These syconia had ripened completely but displayed no exit channels. On dissection, seeds were discovered in both seed and gall flowers and there was a complete lack of insects. These seeds germinated normally. Since selfing within the syconium is excluded, the origin of these seeds is uncertain. If the flowers from these syconia were in fact pollinated by sterile females, remains of the insects would have been found. The only remaining suggestion appears to be that the seeds were produced by some form of parthenogenesis.

DISCUSSION

Flowering in the genus *Ficus,* must involve a tremendous output of energy since each crop of syconia produces many thousands of flowers. Much of this energy becomes spent in the maintenance of a supply of pollinators. Hence, flowering represents a compromise between seed production and the provision of an adequate supply of pollinators. It is therefore of obvious advantage to produce large numbers of small reduced flowers. Seed and gall flowers have evolved as a long term safety mechanism to effectively maintain this fine balance between the production of seeds and pollinators. However, it is important to note that the variation between seed and gall flowers is essentially one of gross morphology and there is no bimodal distinction between them. Occasionally, seeds occur in short styled flowers, whereas fairly long styled flowers produce galls. The continuous range of style lengths does ensure that a percentage of the ovaries remains beyond the reach of the ovipositors of the primary sycophiles. This was determined by measurement of random samples of 200 styles of female flowers and wasp ovipositors.

The developmental cycle of the syconium of *F. capensis* is very similar to that described for *F. sycomorus* (Galil & Eisikowitch, 1968b). However, the very rapid increase in diameter of the syconium during the ripening or postfloral phase has not been emphazised by previous workers. Furthermore, the interfloral phase may be differentiated into two equal sub-phases (C_1 and C_2). During the first half of the interfloral phase (C_1) growth continues at a more or less normal rate while during the second half (C_2) increase in size of the hard green syconia is negligible. C_2 may therefore be regarded as a resting period during which the seed walls harden considerably and the wasps pupate within their galls.

Asynchronous flowering in *F. capensis* ensures that receptive stages of figs are always available for infection by wasps that leave the male or D-phase syconia. This is essential since wasps are believed to be non-feeding and fairly short lived. Females of *C. capensis* survived in the laboratory for periods of 35–50 hours. Sometimes only a single branch on a tree may bear syconia and this usually represents less than 10% of the normal crop. This 'false fruiting' helps to ensure the availability of some syconia in between normal crops, so that, pollinator supplies are successfully maintained. It is interesting to note that the presence of such syconia has also been observed for *F. natalensis* Hochst., in the Durban area.

Although outbreeding may be the general rule in the genus *Ficus,* crop-overlap could result in wasps from male phase syconia pollinating female phase syconia on the same tree. The occurrence of crop-overlap has not been reported by previous workers but close observation might reveal that this is of a more widespread occurrence. Certainly, some inbreeding must occur in populations of *F. capensis.* Since each species has become so specialized a degree of inbreeding can be an advantage in the maintenance of the species. In general, there appears to be a slight increase in fruiting during the warm rainy season with many trees fruiting continuously or displaying degrees of crop overlap. Hence, there will be an ample build-up of seeds and pollinators during this period.

The developmental cycles of the wasps and the syconia are, of necessity, perfectly synchronized. The behavioural patterns of the pollinating wasps viz. pocket filling and pocket emptying ensures successful pollination of receptive flowers. There are two basic reasons for *S. cyclostigma* being ineffective in pollination. Firstly, there are no specialized pollen carrying structures and secondly, the elaborate grooming behaviour of the females reduces the probability of pollen adhering to the body of the insect. On the other hand, pollination by *C. capensis* is very successful since it is a deliberate act resulting from a distinct behavioural sequence. It is important to note that pollination of a few flowers by *S. cyclostigma* cannot be totally excluded. However, the fact that syconia containing exclusive populations of *S. cyclostigma* were completely seedless does indicate that this insect does not affect pollination. Although syconia with unpollinated flowers normally abort, they may persist and ripen if infected by *S. cyclostigma*. Non-infected flowers in such syconia degenerate rapidly. Unlike reports on *S. sycomori* (Galil, Dulberger & Rosen, 1969) in the Middle East, the males of *S. cyclostigma* do not engage in the preparation of an exit channel. Therefore, in the absence of males of *C. capensis*, the entire vespid fauna remains entrapped and perishes within the syconium.

Most of the secondary sycophiles in *F. capensis* are believed to be inquilines i.e. they do not induce gall formation but parasitize existing galls. As such, they do not influence the number of seeds produced per syconium. However, they are unwelcome as they might parasitize galls of *C. capensis* thus causing reduction of the population. Individuals of *Sycophila* sp. and *Camarothorax* sp. develop in enlarged galls with thickened angular walls. These galls usually occur in clumps with gall formation occurring in both short and long styled flowers. It therefore appears that these genera of secondary sycophiles are able to induce gall formation. The elaborate sexual dimorphism present in most sycophilous wasps is lacking in *Sycophila* sp. and *Camarothorax* sp.

The ratios of the different species of wasps occurring in the syconia tend to vary greatly. This would obviously be influenced by availability of the different species of wasps during the receptive and interfloral periods when egg-laying occurs. It is therefore not uncommon to find a crop producing a high percentage of a particular species and exceptionally large populations of *S. cyclostigma* were observed on a number of occasions. Population ratios also vary from one syconium to another within a single crop. In general, however, end of crop syconia produce a very poor population of primary sycophiles. Such syconia mostly contain secondary sycophiles with *Apocrypta* sp. being very common. Since these syconia develop slightly later than the main crop, there are at any one time only a few at the correct interfloral phase for infection by secondary sycophiles. As a result of this, these syconia become heavily infected with the eggs of the available inquilines which then develop at the expense of the primary sycophiles.

A particularly interesting feature in *F. capensis* is the production of geocarpic syconia. These may occur at the soil surface, but are very often buried in the subsurface layers. It was found that geocarpic figs become pollinated and produce viable seeds. Clear knowledge as to how the pollinating wasps gain access to these syconia is completely lacking. Corner (1978) has speculated that wasps might burrow, that geocarpic syconia become exposed by activity of other larger animals, or, that syconia only become buried after pollination has taken place. The last suggestion cannot be accepted for *F. capensis* as young prereceptive syconia may be truly geocarpic. In all cases studied, a colony of ants was found to be associated with the geocarpic syconia. The likelihood of wasps reaching the syconia through the ant burrows thus cannot be totally outruled. However, it is definitely known that ants are predators of fig wasps. As wasps leave male phase syconia through the ostiole they are often snatched up by the waiting workers. These workers may later enter the syconium and carry out the wingless male wasps. Therefore, if wasps had to gain access to the syconia through the ant burrows, they may only do so when ant activity is at a standstill.

The pollination syndrome of the genus *Ficus* probably represents one of the most unique animal-plant relationships existing in nature. The pollination movements of the insects appear to have no short term advantage to the pollinating wasps and is an instinctive behavioural sequence (Galil & Eisikowitch, 1969). One of the most interesting unanswered questions in the pollination story is what attracts the wasps to the syconium. It is very likely to be an olfactory stimulus that attracts the correct pollinator. At present the possibility of investigating the chemical nature of the various components of the syconium is being undertaken. The only other well documented case of ethodynamic pollination is that of the Yucca plant and its pollinating moth (Riley, 1892).

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Studies of diagnostic features in the genus *Hypoxis* L. (Hypoxidaceae R. Br.) on the Witwatersrand

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ABSTRACT

In an attempt to clarify specific concepts in the genus *Hypoxis* L. on the Witwatersrand it was found that diagnosis depends mostly on vegetative characters, particularly the habit, leaf vesture and venation, and the structure of the inflorescences.

The relevant criteria are discussed in relationship to the Witwatersrand species, where eleven species and seven varieties are recognized: *H. rigidula* Bak. (a) var. *rigidula,* (b) var. *pilosissima* Bak.; *H. acuminata* Bak.; *H. filiformis* Bak.; *H. obtusa* Burch.; *H. neliana* Schinz; *H. latifolia* Hook. f.; *H. galpinii* Bak.; *H. multiceps* Buch. ex Bak.; *H. interjecta* Nel; *H. rooperi* Moore; *H. argentea* Harv. ex Bak. (a) var. *argentea,* (b) var. *sericea* Bak.; and two varieties which constitute *comb. et stat. novs,* unpublished as yet.

RÉSUMÉ

ÉTUDE DES CARACTÈRES DIAGNOSIQUES DANS LE GENRE HYPOXIS *L. (HYPOXIDACEAE R. BR.) DANS LE WITWATERSRAND*

En tentant de clarifier les concepts spécifiques du genre Hypoxis *L. dans le Witwatersrand, on a constaté que la diagnose se définit surtout par des caractères végétatifs, particulièrement le port, la nervation et l'indumentation de la feuille, ainsi que de la structure des inflorescences.*

Ces critères sont appliqués pour la distinction des espèces du Witwatersrand, où onze espèces et sept variétés sont reconnues: H. rigidula *Bak. (a) var.* rigidula, *(b) var.* pilosissima *Bak.;* H. acuminata *Bak.,* H. filiformis *Bak.;* H. obtusa *Burch.;* H. neliana *Schinz;* H. latifolia *Hook. f.;* H. galpinii *Bak.;* H. multiceps *Buch. ex Bak.;* H. interjecta *Nel;* H. rooperi *Moore;* H. argentea *Harv. ex Bak. (a) var.* argentea, *(b) var.* sericea *Bak.; et deux variétés qui constituent* comb. et stat. novs *non encore publié.*

1 INTRODUCTION

Hypoxis L. is the type genus of the small family Hypoxidaceae R.Br. with distribution in the warmer regions of all the continents except Europe. In southern Africa it is well represented in the summer rainfall area, but absent in the flora of the Western Cape.

Quite recently (Walford, 1978), medical interest has arisen in certain *Hypoxis* species which were found to yield compounds useful in treatment of prostate cancer and of rheumatism. Further research is going on.

The genus was comprehensively treated by Baker (1878), and Baker's descriptions of the South African species were included in Flora Capensis (1896). The family was revised by Nel (1914). A partial revision of the Natal species has been recently carried out by Wood (1976, unpub.).

My studies were concerned with an attempt to clarify the specific determinations in the genus on the Witwatersrand. Here, for a few weeks in spring, *Hypoxis* is a dominant element in grassland; however, little is known about the genus. Before any taxonomic treatment, I had to gain information on population structures, life cycles, morphology and anatomy of the taxa. Then I was able to correlate these data with the accepted nomenclature available in literature and herbarium collections. In the present paper I want to discuss some of my findings.

2 DIAGNOSTIC CHARACTERS

It soon became evident that in this genus diagnosis at specific level depends mostly on vegetative characters. The habit, leaf vesture and anatomy, and the structure of the inflorescences yield the most important criteria.

2.1 *Gross morphology*

The plants have a simple 'streamlined' appearance: a perennial corm with contractile roots and an annual complement of basal leaves and slender unbranched axillary peduncles. The leaves and peduncles emerge trifariously (1/3 phyllotaxis) from the corm apex.

2.1.1 *Rootstock. Hypoxis* corms generally do not form offsets. They grow vertically upwards, continuously pulled deep into the ground by their contractile roots. Above ground there is a single shoot.

In two Witwatersrand species, *H. acuminata* (Fig. 1A) and *H. galpinii,* the rootstock after a time spreads horizontally, forming short stolons. Each has a cormlike structure with a shoot at the apex. Above ground arises a tussock of several shoots, often as many as 20–40.

2.1.2 *Habit.* The length of mature shoots covers a range from 80–1400 mm. Three groups can be distinguished.

(a) Shoots spreading trifariously from the base. Here belong species with falcate leaves tightly stacked above each other in three ranks at angles of 120°: the large *H. rooperi* (Fig. 1B) and the small *H.*

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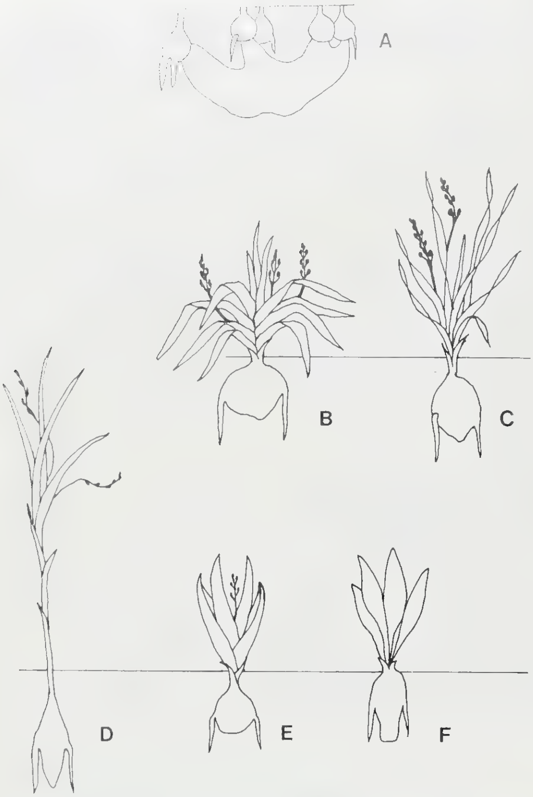

FIG. 1.—Branching rootstock. A, *Hypoxis acuminata* (× ½), trifarious habit; *H. rooperi* (× 1/5); C, *H. obtusa* (× 1/5), pseudostem; D, *H. rigidula* (× 1/5), funnel-shaped shoots; E, *H. galpinii* (× 1/5); F, *H. multiceps* (× 1/5).

argentea. Or shoots not so strictly trifarious, leaves not stacked, not falcate, but first recurved, and later in season spirally twisting upwards: *H. obtusa* (Fig. 1C).

(b) Leaves emerge from the ground in a trigonal leaf column sheathed by cataphyll bases so that a pseudostem is formed (Fig. 1D).

The pseudostems are as wide in diameter as the emerging leaves in *H. rigidula,* the tallest species in the genus, with pseudostems up to 200 mm long; the medium sized *H. acuminata* and the small *H. filiformis* in which the pseudostem is often absent.

In *H. neliana* the pseudostem is wider than the leaves, though it is only 10–20 mm long.

(c) Funnel shaped shoots. Leaves grow vertically upwards, only slightly separating from each other so that the shoot is wider above, in the shape of a funnel. In *H. latifolia,* a large species with leaves widest in the genus, leaves reach 100 mm in width. In the medium sized *H. galpinii* (Fig. 1E) the leaves when mature are connivent on the top.

In *H. multiceps* (Fig. 1F) and *H. interjecta* towards end of the season leaf bases narrow down and form pseudopetioles. The narrow pseudopetioles at the base and the wide laminae above [illegible]

2.2 *Vesture* (Fig. 2 A,C)

One of the basic characters of the genus is the presence of hair on all the aerial parts of the taxa. The trichomes are unicellular, but pluriseriate (Hummel & Staesche, 1962). That means that a single foot-cell in the epidermis may carry one simple hair, or one two-armed hair, or a stellate hair with 3–6 arms, or hair fascicled, with up to 18 arms.

2.2.1 *Hair orientation.* The hair may be appressed to the surface or patent. Patent hair produces woolly-effect on *H. rigidula* var. *pilosissima,* sericeous sheen on *H. argentea* leaves; densely fascicled hair on leaf margins forms white bands outlining the contours of the leaves in *H. obtusa* and *H. multiceps.*

2.2.2 *Hair topography.* On the inflorescences of *Hypoxis* hair is present in all species. The distribution of hair on the leaves varies. One Witwatersrand species, *H. interjecta,* has leaves totally glabrous. In *H. obtusa* var. *obtusa,* with the fascicled hair on margins, the leaf lamina is glabrous. In *H. rooperi* the lamina is densely covered with long hairs, but hair on the margins is sparse, fringelike. On the lamina of *H. rigidula* var. *rigidula* the hair is appressed in intercostal grooves; in *H. multiceps* it is found mostly above the veins. *H. filiformis* and *H. galpinii* have thin, sparse hair on the lamina and margins.

2.3 *Epidermis*

2.3.1 *Stomata.* The stomata of *Hypoxis* are mostly paracytic, but tetracytic in *H. argentea* and *H. galpinii,* and sunken in *H. filiformis.* The cuticle on subsidiary cells is smooth in *H. argentea,* outlined by a ridge in *H. rigidula, H. acuminata* and *H. neliana,* puckered in soft folds in *H. rooperi* and *H. obtusa* or covered by fine parallel striations in *H. multiceps* (Fig. 2B), *H. interjecta* and *H. galpinii.*

2.3.2 *Inclusions.* The taxa have many idioblasts with bundles of raphids, rodlike crystals of calcium oxalate monohydrate. In the epidermis of *H. filiformis, H. neliana* and *H. obtusa* var. *nitida* I found tetragonal crystals of calcium oxalate dihydrate, in short sequences over the veins. In *H. obtusa* var. *obtusa,* in the long parallel rows of epidermal cells over the veins, each cell contains such crystals. The leaves are stiff, coriaceous.

2.4 *Venation: leaf anatomy* (Fig. 3)

2.4.1 *Veins in transection.* The leaves of *Hypoxis* have parallel veins of uneven thickness, some very prominent. In transection they are seen as strands or girders (Metcalfe, 1960). The strands are small bundles of vascular tissue, surrounded by a bundle sheath. In girders the circumvascular sclerenchyma extends across the width of the lamina to the epidermis.

The strands are usually oval; they do not affect the leaf outline. The girders are T-shaped, rectangular or crescent-shaped. On the leaf surface T-girders protrude as wide, prominent ribs; the rectangular and crescent-shaped girders protrude only slightly.

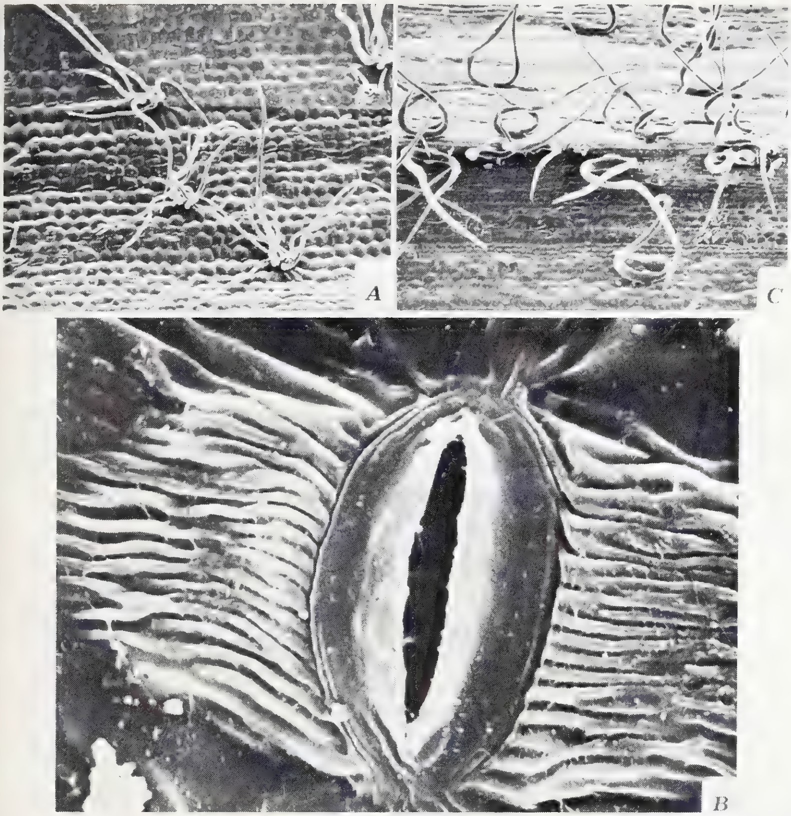

FIG. 2.—Hair: A, *H. multiceps*, stellate hair; C, *H. neliana*, two-armed curling hair (×50). Stoma: B, *H. multiceps* (× 1 500).

2.4.2 *Number and shape of girders.* Very prominent T-shaped girders characterize *H. rigidula* (14–20) and *H. acuminata* (5–6, submarginal).

Rectangular girders occur in *H. obtusa* (60–80), *H. neliana* (8–10), *H. multiceps* (24–50) and *H. interjecta* (24–40). They hardly protrude on the surface and are comparatively uniform in appearance. In *H. galpinii* (34–60) and *H. argentea* (4) two large girders are in quartile position, halfway between the keel and the margin: these girders are prominent only on the adaxial surface, and there the leaf shallowly folds back, the girder accentuating the fold.

Crescent-shaped girders are found in *H. rooperi* (30–48) and *H. latifolia* (12–15, very widely spaced). They alternate with strands in 1: 2 pattern.

2.5 *Structure of the inflorescences* (Fig. 4)

2.5.1 *The inflorescence.* The basic shape of *Hypoxis* inflorescence cannot be easily described by conventional terminology. Müller-Doblies (1977) defines it as a transitional stage between a rhipidium and a bostryx. The monochasial peduncles arise in leaf axils, in similar trifarious arrangement. In transection the peduncle is ancipitous, or flattened into a quasi rectangular shape, or crescent-shaped (canaliculate). On its upper part is a simple racemose inflorescence of pedicellate or rarely sessile flowers, each flower subtended by a bract.

2.5.2 *Flower arrangement.* The arrangement of flowers on the peduncle is an important diagnostic feature. Three types are distinguished:

(a) A slender sinuous ancipitous peduncle with alternate sessile or subsessile flowers. Flowers are spirally arranged, many, 2–18, *H. rigidula;* or few, 2–6, *H. acuminata,* or 4–11, distichously arranged, *H. galpinii.*

(b) In several species short erect peduncles bear flowers in pairs, in opposite arrangement. A two-flowered inflorescence resembles the letter Y, each flower on a long pedicel representing an upper branch of the Y, the peduncle forming the base. A four-flowered inflorescence has two Y-shaped tiers, one above the other, in decussate arrangement. Rarely a six-flowered inflorescence can be found, with flower pairs in three such tiers. The upper tier is sometimes reduced to one flower, forming a 3- to 5-flowered structure.

Peduncle slender, ancipitous; pedicels in each pair equal: 2–4 flowers, pedicels 10–30 mm, *H. argentea;* 2–5 flowers, pedicels 13–25 mm, *H. interjecta* and *H. multiceps.*

Peduncle stout, flattened; pedicels unequal: 1–3 flowers, pedicels 10–14 mm, *H. neliana.*

Peduncle slender, canaliculate; pedicels unequal, one flower usually sessile: (1)–2–(3) flowers, pedicels 0–14 mm, *H. filiformis.*

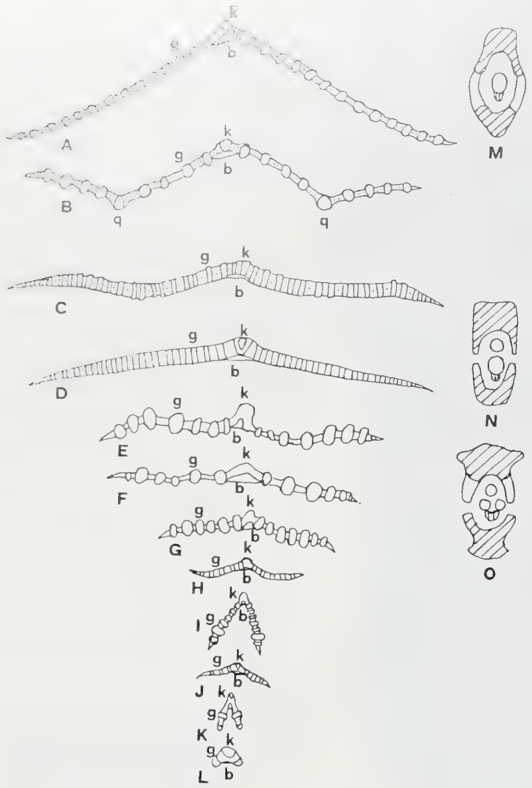

FIG. 3.— Leaf venation. A – L, leaf transections (× 3). A, *H. rooperi,* B, *H. galpinii;* C, *H. obtusa* var. *'nitida',* D, *H. obtusa* var. *obtusa;* E, *H. rigidula* var. *'hemerocallidea';* F, *H. rigidula* var. *pilosissima;* G, *H. rigidula* var. *rigidula;* H. *H. multiceps* and *H. interjecta;* I, *H. acuminata;* J. *H. neliana;* K, *H. argentea;* L, *H. filiformis.* M–O, fibrous girders (× 30): M, crescent-shaped (in leaves A, B, H); N, crossbar-shaped (in leaves C, D, J, K, L); O, T-shaped (in leaves E, F, G, I).

(c) Stout, flattened peduncles, with flowers in mixed sequences, the two lowermost opposite, the rest opposite and alternate, or in whorls of three. Flowers 5–13; pedicels 5–20 mm long, *H. obtusa;* flowers 4–13; pedicels 15–25 mm long, *H. rooperi.*

2.6 *Colour*

There is little interspecific variation in colour. In nearly all the taxa the corms exude yellow mucilage when sectioned; the aerial parts are green and dry beige-brown; the flowers are yellow.

However, there are solitary exceptions. The corms of *H. argentea* are white in section; the peduncles and pedicels in this species are tinged maroon. *H. rigidula* var. *hemerocallidea* has purple pseudostems. When dried *H. galpinii* leaves turn red, and in *H. obtusa* var. *obtusa* the dried foliage is silvery grey. *H. filiformis* at times produces whitish flowers.

3 CONCLUSIONS

On the basis of my findings I have recognized the following 11 species and 7 varieties of *Hypoxis* present on the Witwatersrand:

H. rigidula Bak.
  (a) var. *rigidula*
  (b) var. *pilosissima* Bak.
  (c) var. *hemerocallidea* (Fisch. & Mey.) Heid., *comb. et stat. nov.**
H. acuminata Bak.
H. filiformis Bak.
H. obtusa Burch.
  (a) var. *obtusa*
  (b) var. *nitida* (Verdoorn) Heid., *comb. et stat. nov.**
H. neliana Schinz
H. latifolia Hook. f.
H. galpinii Bak.
H. multiceps Buch. ex Bak.
H. interjecta Nel
H. rooperi Moore
H. argentea Harv. ex Bak.
  (a) var. *argentea*
  (b) var. *sericea* Bak.

A key and the descriptions of the species are to be published at a later date.

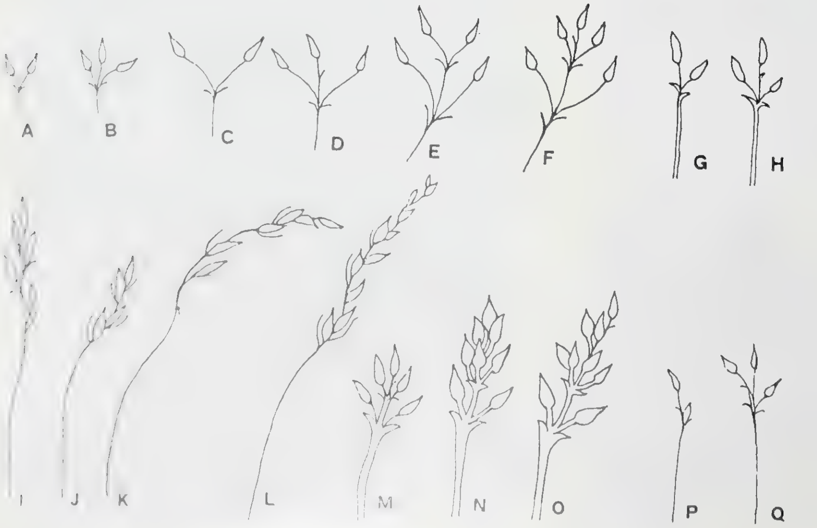

FIG. 4.—Inflorescences (× 1/4). A, B, *H. multiceps* and *H. interjecta;* C, D, E, F, *H. argentea* (C is a Y-shaped inflorescence); G, H, *H. neliana;* I, *H. galpinii;* J, *H. acuminata;* K, *H. rigidula* var. *rigidula;* L, *H. rigidula* var. *pilosissima* and var. *'hemerocallidea';* M, N, O, *H. obtusa* and *H. rooperi;* P, Q, *H. filiformis.* Ancipitous peduncles — single line; flattened peduncles — double line.

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* This *comb. et stat. nov.* will be formally published elsewhere.

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Bothalia 14, 3 & 4: 895–899 (1983)

Anatomy of *Sarcocaulon*

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ABSTRACT

The anatomy of the leaf blade, petiole, stem and root of the genus *Sarcocaulon* (DC.) Sweet is discussed. On the basis of the leaf anatomy, the four sections recognized by Moffett (1979) can be identified: section *Denticulati* (dorsiventral leaves), section *Multifidi* (isobilateral leaves and adaxial and abaxial palisade continuous at midvein), section *Crenati* (isobilateral leaves, short curved trichomes and glandular hairs), section *Sarcocaulon* (isobilateral leaves and glandular hairs only). The anatomy of the stem is typically that of a herbaceous dicotyledon with a thick periderm. The root structure shows that the function of the root is not food storage.

RÉSUMÉ

L'ANATOMIE DES SARCOCAULON

L'anatomie du limbe foliaire, du pétiole, de la tige et de la racine du genre Sarcocaulon *(DC.) Sweet est discutée Sur base de l'anatomie de la feuille, les quatre sections reconnues par Moffett (1979) peuvent être identifiées: section* Denticulati *(feuilles dorsiventrales) section* Multifidi *(feuilles isobilatérales et tissu palissadique adaxial et abaxial continue au niveau de la nervure médiane), section* Crenati *(feuilles isobilatérales, trichomes courts et courbés et poils glandulaires), section* Sarcocaulon *(feuilles isobilatérales et poils glandulaires seuls). L'anatomie de la tige est typiquement celle d'une dicotylédone herbacée avec un périderme épais. La structure de la racine montre que celle-ci ne joue pas le rôle d'une réserve alimentaire.*

INTRODUCTION

Sarcocaulon known by the common name 'Bushman's Candle' is one of the five genera belonging to the family Geraniaceae. The other four are *Geranium, Pelargonium, Monsonia* and *Erodium.*

Sarcocaulon plants are fleshy short-stemmed shrublets covered with a hard waxy bark which is inflammable due to being impregnated with wax. The root system is formed by a primary root and lateral roots. Leaves are long or short petioled with the long petioles persisting as spines. The short petioled leaves occur singly or in tufts in the axils of the spines. The leaves are simple or compound with the nature of the leaf margin of taxonomic importance. Moffett (1979) divided the genus into four sections primarily on the nature of the leaf margin. The following sections and species were recognized by Moffett (1979):

Section *Sarcocaulon* (leaf blade without lateral incisions). *S. camdeboense, S. l'heritieri, S. patersonii, S. salmoniflorum, S. vanderietiae.*

Section *Crenati* (leaf blade with lateral incisions, leaf unsegmented and leaf margin lobed). *S. ciliatum, S. crassicaule, S. flavescens.*

Section *Denticulati* (leaf blade with lateral incisions, leaf unsegmented and leaf margin not lobed). *S. inerme, S. marlothii, S. mossamedense.*

Section *Multifidi* (leaf segmented). *S. herrei, S. multifidum, S. peniculinum.*

The 14 southern African species are distributed over the more arid areas, ranging from the eastern Cape to southern Angola. The majority of species occur near the mouth of the Orange River. The plants grow in extremely hot, dry areas, remaining entirely leafless throughout most of the year. The leafless plants may produce an occasional flower (Glass & Foster, 1970), but the plants only produce leaves after sufficient rain. After such rains, the plants are capable of bursting into flower and leaf almost immediately.

MATERIAL AND METHODS

Material from all the species except *S. inerme* and *S. peniculinum* was investigated.

The material used was obtained from plants in their natural habitats and plants collected and planted in the Botanical Garden of the University of the Orange Free State. The material was fixed in F.A.A., dehydrated by the tertiary butyl alcohol method (Gray, 1958), embedded in Histosec wax and sectioned at 10 μm. The sections were stained in Safranin and Fast Green and mounted in Entellan.

Leaves prepared for the scanning electron microscope were fixed in 3% gluteraldehyde in phosphate buffer (pH, 7,0), post-fixed in 1% osmium tetroxide, dehydrated in ethyl alcohol, critical point dried and sputter coated with gold.

RESULTS AND DISCUSSION

Anatomy of the leaf

Trichomes

Glandular and non-glandular unicellular hairs occur on the leaves. The glandular hair is found on all the species. It consists of a short uniseriate stalk of three cells and a unicellular spherical head (Fig. 1). The non-glandular unicellular trichomes are of two basic types, namely short curved trichomes and long straight trichomes (Figs 2 & 3). The short curved trichomes are found in *S. ciliatum, S. crassicaule, S. flavescens, S. herrei* and *S. multifidum.* The long trichomes are only present in *S. herrei* and *S. multifidum.*

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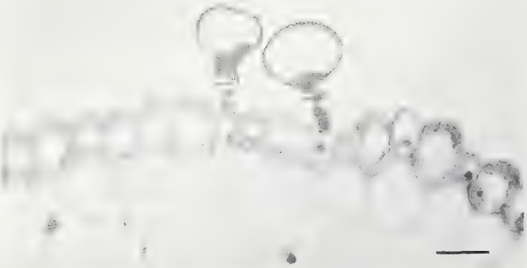

FIG. 1.—Part of a cross section through the petiole of *Sarcocaulon marlothii* to show the glandular hair. Bar = 20 μm.

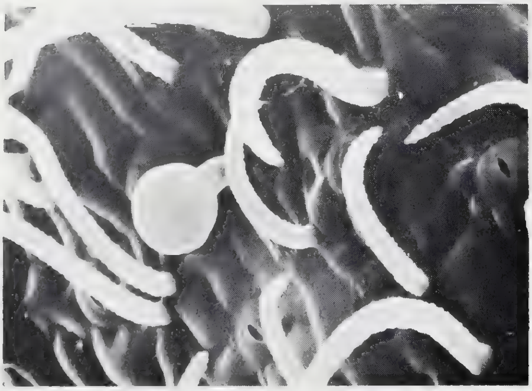

FIG. 2.—Scanning electron micrograph of glandular hair and curved trichomes on leaf of *Sarcocaulon multifidum*. Bar = 10 μm.

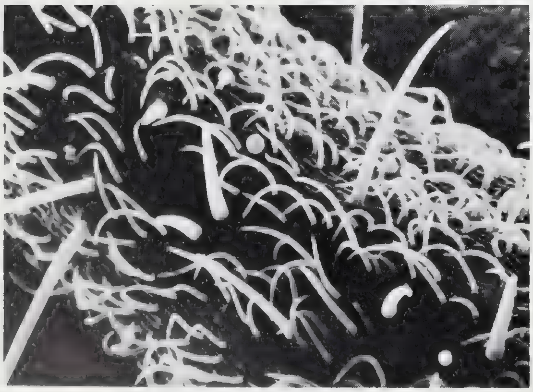

FIG. 3.—Scanning electron micrograph of glandular hairs, curved trichomes and straight trichomes on leaf of *Sarcocaulon multifidum*. Bar = 100 μm.

According to the trichomes present two of the four sections recognized by Moffett (1979) can be identified. These are section *Crenati* with glandular hairs and short curved trichomes and section *Multifidi* with glandular hairs and both types of non-glandular unicellular trichomes. In section *Sarcocaulon* and section *Denticulati* only glandular hairs are found.

Lamina

Isobilateral in all the species, except *S. marlothii* and *S. mossamedense* where the leaf structure is dorsiventral. A thick cuticle is present. The adaxial and abaxial epidermal cells are of more or less the same size both containing cells of unequal size. Anomocytic stomata are found on both upper and lower surfaces of the leaf (amphistomatic leaf) and are on the same level as the other epidermal cells. The pores are irregularly orientated in surface view.

Mesophyll is differentiated into palisade parenchyma and spongy parenchyma. In the dorsiventral leaves (Fig. 4) *(S. marlothii* and *S. mossamedense)* the palisade consists of one cell layer and is not continuous above the main vein. The palisade parenchyma is well developed and in some cases can occupy at least half the thickness of the mesophyll.

In the isobilateral leaves (Fig. 5) the adaxial and abaxial palisade consists of two cell layers with the inner palisade layer consisting of shorter cells. The adaxial palisade layer is usually better developed. In *S. herrei* and *S. multifidum,* the two examples with compound leaves, the adaxial and abaxial palisade parenchyma is continuous at the midvein (Fig. 6). In the other species with isobilateral leaves, the abaxial palisade is always interrupted at the main vein but the adaxial palisade is continuous (Fig. 7) or interrupted in the same species. In the majority of material examined the palisade parenchyma was continuous.

Vascular bundles are collateral with each vein surrounded by a parenchyma sheath. On the abaxial side of the vascular bundle the sheath cells may be sclerenchymatous. A few fibres may be present between the sheath and the phloem. The parenchyma cells internal to the abaxial epidermis are often sclerenchymatous.

Calcium oxalate crystals in the form of druses are common in the mesophyll.

Based on the anatomy of the lamina the two sections *Denticulati* and *Multifidi* can be identified. However, in combination with the trichomes, all four sections recognized by Moffett (1979) can be identified. These are section *Denticulati* with dorsiventral leaves, section *Multifidi* with isobilateral leaves and adaxial and abaxial palisade

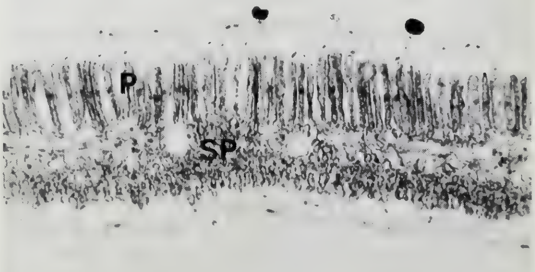

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FIG. 4.—Part of a cross section through dorsiventral lamina of *Sarcocaulon mossamedense*. P, palisade parenchyma; SP, spongy parenchyma. Bar = 100 μm.

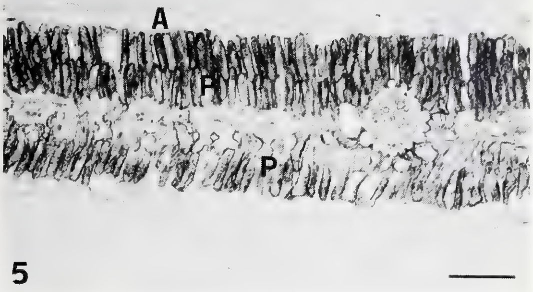


FIG. 5.—Part of a cross section through isobilateral lamina of *Sarcocaulon camdeboense*. A, adaxial epidermis; P, palisade parenchyma. Bar = 100 μm.

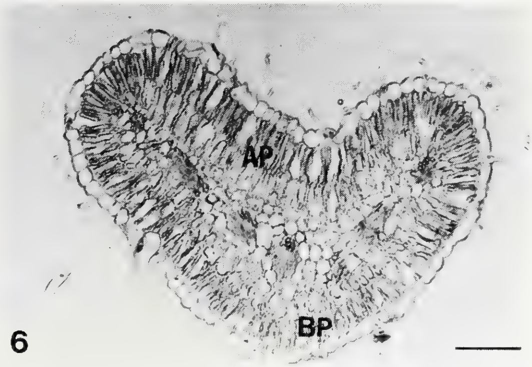


FIG. 6.—Cross section through isobilateral leaf of *Sarcocaulon multifidum* to show the continuous adaxial (AP) and abaxial palisade (BP) at midvein. Bar = 100 μm.

continuous at midvein, section *Crenati* with isobilateral leaves, short curved trichomes and glandular hairs and section *Sarcocaulon* with isobilateral leaves and glandular hairs only.

Petiole

The anatomy of the petiole is the same in all the species. The outline is circular and a thick cuticle present. The epidermis is composed of thick-walled cells. The cortex is parenchymatous with 1 or 2 cell layers subjacent to the epidermis often chlorenchymatous. Druse crystals are common in the cortex. Three (Fig. 8) or four (Fig. 9) vascular bundles are grouped together in the centre of the petiole with the fourth bundle usually smaller. The vascular bundles are each partially subtended or completely surrounded by sclerenchyma.

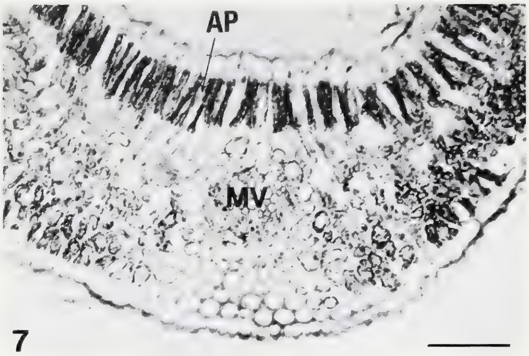
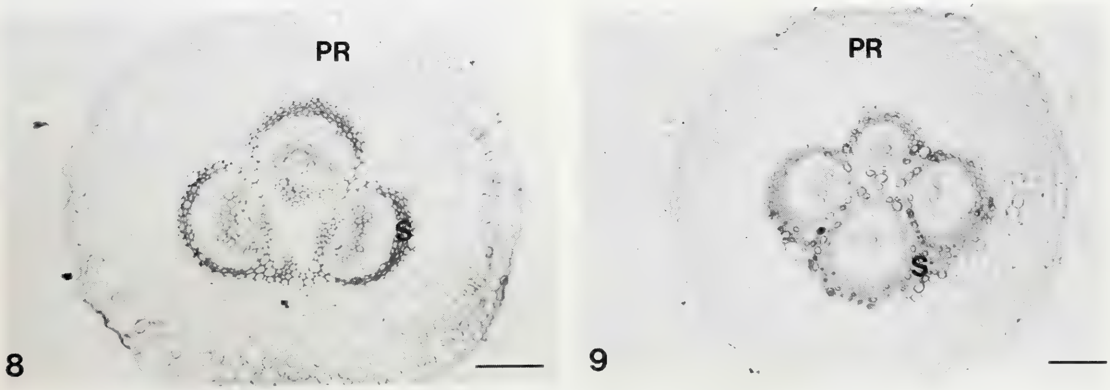


FIG. 7.—Cross section through midvein of *Sarcocaulon flavescens* to show the continuous adaxial palisade (AP). MV, midvein. Bar = 100 μm.

Spine (thorn)

The spine is formed from the long petiole after the lamina falls off. The anatomy of the spine resembles that of the petiole except that the four vascular bundles are arranged in a circle around the pith (Fig. 10). Between each of the four vascular bundles a smaller vascular bundle is often present. The thorn forms by lignification of the cells. Lignification begins around the vascular bundles and continues from the inside to the outside. The outer cortical layers may be lignified and persistent or are cast off together with the epidermis.

The four sections recognized by Moffett (1979) can be identified from leaf anatomy. Section *Denticulati* with dorsiventral leaves, section *Multifidi* with isobilateral leaves and adaxial and abaxial



FIGS 8 & 9.—Cross section through the petiole of *Sarcocaulon crassicaule* with three (Fig. 8) and four (Fig. 9) vascular bundles. PR, parenchyma; S, sclerenchyma. Bar = 100 μm.

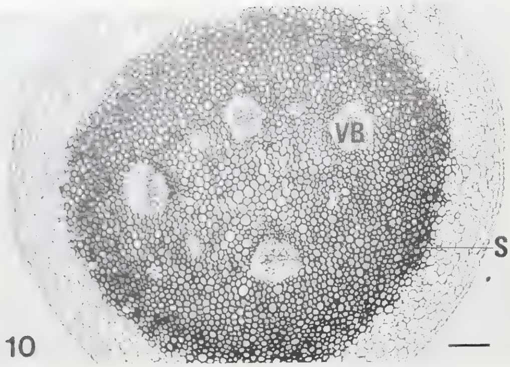


FIG. 10.—Part of a cross section through the spine of *Sarcocaulon crassicaule* to show the four vascular bundles in lignified tissue. S, sclerenchyma; VB, vascular bundle. Bar = 100 µm.

palisade continuous at midvein, section *Crenati* with isobilateral leaves, short curved trichomes and glandular hairs and section *Sarcocaulon* with isobilateral leaves and glandular hairs only.

For plants growing in extremely hot dry areas, the leaves do not appear xerophytic with the stomata on the same level as the epidermal cells. Xerophytic features of the leaves are, however, the strongly developed palisade, small intercellular spaces, thick cuticle and dense covering of trichomes in some species. Although more xeromorphic features could be expected, it must be kept in mind that the leaves develop only after sufficient rain and are lost under unfavourable conditions.

Anatomy of the stem

The anatomy of the stem is very similar in all species. The stem is typically that of a herbaceous dicotyledon with collateral vascular bundles separated by wide parenchymatous medullary rays. The stem is covered by a layer of cork which peels off easily. A phellogen is formed early. In seedlings the phellogen originates in the subepidermal parenchyma while the cotyledons are still on the plant. The phellogen produces a conspicuous phellem to the outside and up to six layers of phelloderm cells toward the inside (Fig. 11)

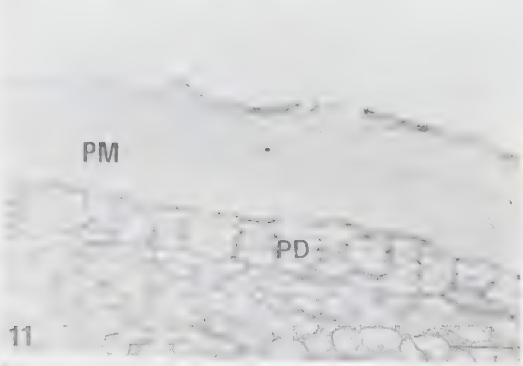


FIG. 11.—Part of a cross section through the stem of *Sarcocaulon flavescens* to show the phellem (PM) and phelloderm (PD). Bar = 100 µm.

The cortex consists of parenchyma cells containing druse crystals of calcium oxalate, tannin and abundant starch grains. The parenchyma cells immediately beneath the phelloderm are rich in chloroplasts, whereas the rest are filled with starch grains. Internal to the phelloderm, a few brachysclereids are sometimes present.

With secondary growth, a fascicular and interfascicular cambium develops (Fig. 12) The vascular cambium produces secondary xylem and phloem in radially arranged groups. Rays up to six cells wide separate the vascular bundles. Ray cells are often filled with starch grains (Fig. 13). External to the phloem, the pericycle is represented by a few fibres. In some cases, fibres are also present in the primary and secondary phloem.

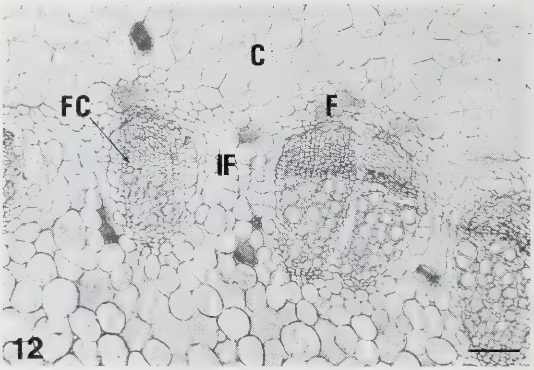


FIG. 12.—Part of a cross section through the stem of *Sarcocaulon flavescens* to show the separate vascular bundles and beginning of secondary growth. C, cortex; F, fibres; FC, fascicular cambium; IF, interfascicular cambium. Bar = 100 µm.

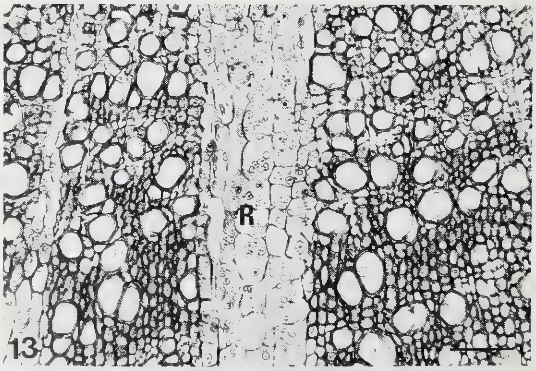


FIG. 13.—Part of a cross section through the secondary xylem of *Sarcocaulon mossamedense* to show the ray cells filled with starch grains. R, ray. Bar = 100 µm.

The pith is similar in structure to the cortex.

The ability of the plants to survive the long dry seasons can probably be ascribed to the phellem, chloroplast rich parenchyma cells beneath the phelloderm, and the starch grains serving as reserve material.

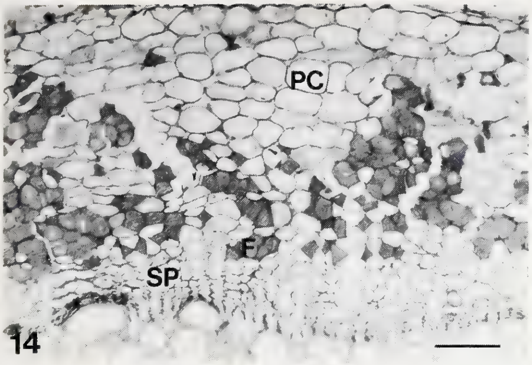


FIG. 14.—Part of a cross section through the root of *Sarcocaulon ciliatum* to show the fibres (F) in the secondary phloem (SP) and pericycle (PC). Bar = 100 μm.

Anatomy of the root

Material of a young root showing the primary state before secondary growth takes place was not available for study. In the secondary state of growth the root consists of primary xylem in the centre surrounded by secondary xylem. The xylem appears homogeneous because of the narrow rays (1–2 cells wide). The secondary phloem and pericycle are rich in fibres (Fig. 14) and are enclosed by the phellem.

From the root structure it is clear that the root's function is not food storage.

ACKNOWLEDGEMENTS

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Intraspecific variability in *Alloteropsis semialata* (R. Br.) Hitchc.

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ABSTRACT

Intraspecific variability in *Alloteropsis semialata* (R. Br.) Hitchc. is shown ultrastructurally with particular regard to the structure of the bundle sheath and the development of the dimorphic chloroplasts in both the C_3 and C_4 forms of this species.

A. semialata is known to possess two distinct anatomical forms — Kranz and non-Kranz — within one species and occurring within a single ecological niche. Kranz and non-Kranz anatomy is known to be correlated with C_4 and C_3 physiology respectively.

Transverse sections of leaf portions taken at midsheath, at the ligule and at midlamina show plastids with different morphologies at different ontogenetic stages. Plastid form is related to the stage of development, the influence of light on the emerging leaf and the C_3 or C_4 form of *A. semialata.* Stages from amyloplast to chloroplast are investigated with regard to fine structure. Leaf transverse sections are examined microscopically and formation of new bundles, chiefly in the lamina is traced. Differences in anatomy and distribution of vascular bundles are more evident in the lamina than in the colourless leaf sheath.

Both C_3 and C_4 forms of *A. semialata* are found to show chloroplast dimorphism in vascular bundle sheath and mesophyll cells. This is shown to differ in the two forms. The specialized chloroplasts of the Kranz sheath are shown to develop in the inner or mestome sheath, and not in the parenchyma sheath as in some other members of the Kranz Panicoideae.

Features of *A. semialata,* such as the double bundle sheath, granal chloroplasts and large numbers of mitochondria in bundle sheath cells, in the C_4 form, question the current classification of this grass as a malate former.

RÉSUMÉ

VARIABILITÉ INFRASPÉCIFIQUE CHEZ ALLOTEROPSIS SEMIALATA *(R. BR.) HITCHC.*

Une variabilité infraspécifique chez Alloteropsis semialata *(R. Br.) Hitchc. est apparente dans son ultrastructure, particulièrement lorsqu'on examine la structure de la gaine du faisceau et le développement des chloroplastes dimorphiques dans les deux formes, C_3 et C_4, de cette espèce.*

*On sait qu'*A. semialata *possède deux formes anatomiques distinctes, 'Kranz' et 'non Kranz' — au sein de la même espèce et dans une même niche écologique. On sait aussi que l'anatomie 'Kranz' et 'non Kranz' est en corrélation avec la physiologie respectivement en C_4 et C_3.*

*Des sections transversales de morceaux de feuilles prélevées au milieu de la gaine, sur la ligule et au milieu du limbe montrent des plastes ayant une morphologie différente aux divers stades ontogénétiques. La forme du plaste est en relation avec le stade de développement, l'éclairement de la feuille qui émerge et la forme C_3 ou C_4 d'*A. semialata. *Les stades de l'amyloplaste au chloroplaste sont examinés quant à leur structure fine. Les sections transversales des feuilles sont soumises à un examen microscopique et la formation de nouveaux faisceaux, surtout dans le limbe, est observée. Les différences dans l'anatomie et la répartition des faisceaux vasculaires sont plus évidentes dans le limbe que dans la gaine foliaire incolore.*

Les deux formes C_3 et C_4 de A. semialata *révèlent un dimorphisme des chloroplastes dans la gaine des faisceaux vasculaires et dans les cellules du mésophylle. Ce dimorphisme est différent dans les deux formes. Les chloroplastes spécialisés de la gaine 'Kranz' se développent dans la gaine interne ou méstome et non dans la gaine parenchymateuse comme chez certains autres membres des Panicoïdées Kranz.*

*Les caractères d'*A. semialata, *tels que la double gaine des faisceaux les chloroplastes à granums et la grand nombre de mitochondries dans les cellules de la gaine des faisceaux, dans la forme C_4, remet en question la classification actuelle de cette graminée dans les producteurs de malate.*

INTRODUCTION

A close correlation has been reported between mature leaf anatomy and the biochemical type of CO_2 fixation in higher plants (Björkman & Berry, 1973; Hattersley, Watson & Osmond, 1977), particularly with regard to distribution and structure of chlorenchymatous tissue. High frequency of chloroplasts in the vascular bundle sheath cells, together with other specialized cytological features, constitutes Kranz anatomy (Carolin, Jacobs & Vesk, 1973; Johnson & Brown, 1973; Downton, 1971), and is one of the characteristics of C_4 photosynthetic plants (Black & Mollenhauer, 1971; Laetsch, 1974). In C_4 plants photosynthetic CO_2 fixation involves a pathway in which the primary products are C_4 dicarboxcyclic acids produced in the mesophyll cells (Hatch & Slack, 1966).

Mesophyll and bundle sheath chloroplasts may show both structural (Hodge, McLean & Mercer, 1955; Johnson & Brown, 1973) and ontogenetic dimorphism (Laetsch & Price, 1969). Chloroplast structure and arrangement within the bundle sheath (such as centripetal or centrifugal disposition of the chloroplasts and the presence or absence of grana) provide important distinguishing features which have been correlated with particular enzymes for decarboxylation of the 4-carbon products, malate

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and aspartate. (Gutierrez, Gracen & Edwards, 1974; Hatch, Kagawa & Craig, 1975).

Many C_3 plants which produce a three carbon compound as the primary product of CO_2 fixation and show non-Kranz anatomy, also possess bundle sheaths in which chloroplasts may be present (Miyake & Maeda, 1978), although in fewer numbers and without Kranz specialization. Whether the C_3 bundle sheath chloroplasts function as mesophyll cells or have a specialized function of their own, remains at present undetermined. From all these facts the structure of bundle sheath cells and the chloroplasts they contain, is seen to be important in both C_3 and C_4 plants.

Vascular bundle sheath structure in the Poaceae is well documented. Bundle sheaths may be double or single. The outer, the inner, or both bundle sheaths may be Kranz (Brown, 1975), or they may show non-Kranz anatomy. These and other specific anatomical features have been correlated with the C_3 (non-Kranz) and C_4 (Kranz) syndrome (Downton & Tregunna, 1968; Smith & Brown, 1973). The C_4 category has been further subdivided according to the carboxylation product, malate or aspartate (Downton, 1970; Kortschak, Hartt & Burr, 1965). C_4 grasses have been classified, according to the predicted dominant decarboxylating enzyme in the bundle sheaths, on the basis of anatomy and cytology alone (Hattersley & Watson, 1976; Ellis, 1977). Structural and biochemical criteria are also considered to reflect phylogenetic and evolutionary tendencies (Brown, 1975) as well as being correlated with ecological distribution patterns of C_3 and C_4 grasses which show different environmental preference (Teeri & Stowe, 1976; Vogel, Fuls & Ellis, 1978).

In much of the anatomical and physiological work done on the C_3/C_4 syndrome the midlamina region of mature leaves has been used. Ontogeny of chloroplasts and vascularization of grass leaves has not been dealt with extensively in the literature. Sharman (1945) deals with the leaf primordium only. Leech, Rumsby & Thomson (1973) and Leech, Thomson & Platt-Aloia (1981), describe plastid division in meristematic cells of young *Zea mays* leaves, but do not follow further plastid development in mature cells. Laetsch & Price (1969) show development of dimorphic chloroplasts in sugar cane, and Hinchman (1972) shows ultrastructural morphology and ontogeny of oat coleoptile plastids. Miyake & Maeda (1978) compare starch in chloroplasts of C_3 and C_4 plants of the Poaceae.

Bundle sheath structure and chloroplast ontogeny is of particular interest in *Alloteropsis semialata*, since this species shows two anatomical forms, Kranz and non-Kranz (Ellis, 1974) occurring within a single environment (Frean, Barrett & Cresswell, 1980). The same authors have shown that non-Kranz and Kranz forms are associated respectively with C_3 and C_4 photosynthetic characteristics.

This unique situation where two anatomical and [illegible] types occur in one species may indicate a [illegible] different forms. The [illegible] morphological variability and wide geographical distribution (Chippindall & Crook, 1976). Within the sample used in this study Frean & Cresswell (1979) have shown that the C_3 form is more pubescent than the C_4 form. (The terms Kranz and C_4, non-Kranz and C_3 are used synonymously throughout this study.)

The aim of this investigation was to compare the development of chloroplasts in young leaves of comparative age in Kranz and non-Kranz forms of *A. semialata* in order to establish the developmental stage at which they show structural divergence.

METHODS

Glabrous (C_4) and pubescent (C_3) plants of *A. semialata*, removed from the same site in Sandton, Transvaal, were established in containers and kept in the open. Tillers considered to be of comparable age were removed from parent tussocks. Voucher specimens were lodged in the Moss Herbarium (J), University of the Witwatersrand, Johannesburg.

The most recently emerged leaves where the ligule is defined only as a ring of hairs, were taken from five C_3 and five C_4 tillers. Sections were taken at three levels; midsheath (colourless), the leaf immediately above the ligule (pale green) and at midlamina (green).

For electron microscopy leaf material was cut into small pieces (2 mm^2) from tissue between midrib and margin. Material was fixed in 2% glutaraldehyde in 0,1 M cacodylate buffer at pH 7,2 for 2 hours, rinsed in buffer and post-fixed in 1% osmium tetroxide for 2 hours. Subsequent treatment consisted of dehydration in a graded alcohol series and embedment in Spurr's resin (Spurr, 1969). Blocks were sectioned at 60–90 nm, using glass knives on a Reichert OM U_2ultra-microtome, stained with Reynolds's (1963) lead citrate enhanced with uranyl acetate and viewed in a JEM 100 S transmission electron microscope.

For light microscopy monitor sections were cut from the same blocks at 1–2 μm, and stained with 1% toluidine blue in 1% borax. Leaf transverse sections were cut on a freezing microtome at 20–25 μm. Presence of starch was confirmed by staining with iodine potassium-iodide.

The C_4 photosynthetic pathway enzymes were extracted as described by Raghavendra & Das (1978) with 1% (w/u) BSA added to the extraction medium. RUBP-carboxylase activity was determined according to the method of Björkman (1968), PEP-carboxylase according to Maruyama, Easterday, Chang & Lane (1966), aspartate aminotransferase and alanine aminotransferase, Edwards & Gutierrez (1972), NADP malic dehydrogenase and NAD/NADP malic enzyme, Raghavendra & Das (1978), and PEP carboxykinase according to Edwards, Kanai & Black (1971). Chlorophyll was determined by the method of Arnon (1949).

RESULTS

The size and position of the most recently emerged leaf on a C_3 and a C_4 tiller is shown in Fig. 1a, b and levels at which sections were taken are

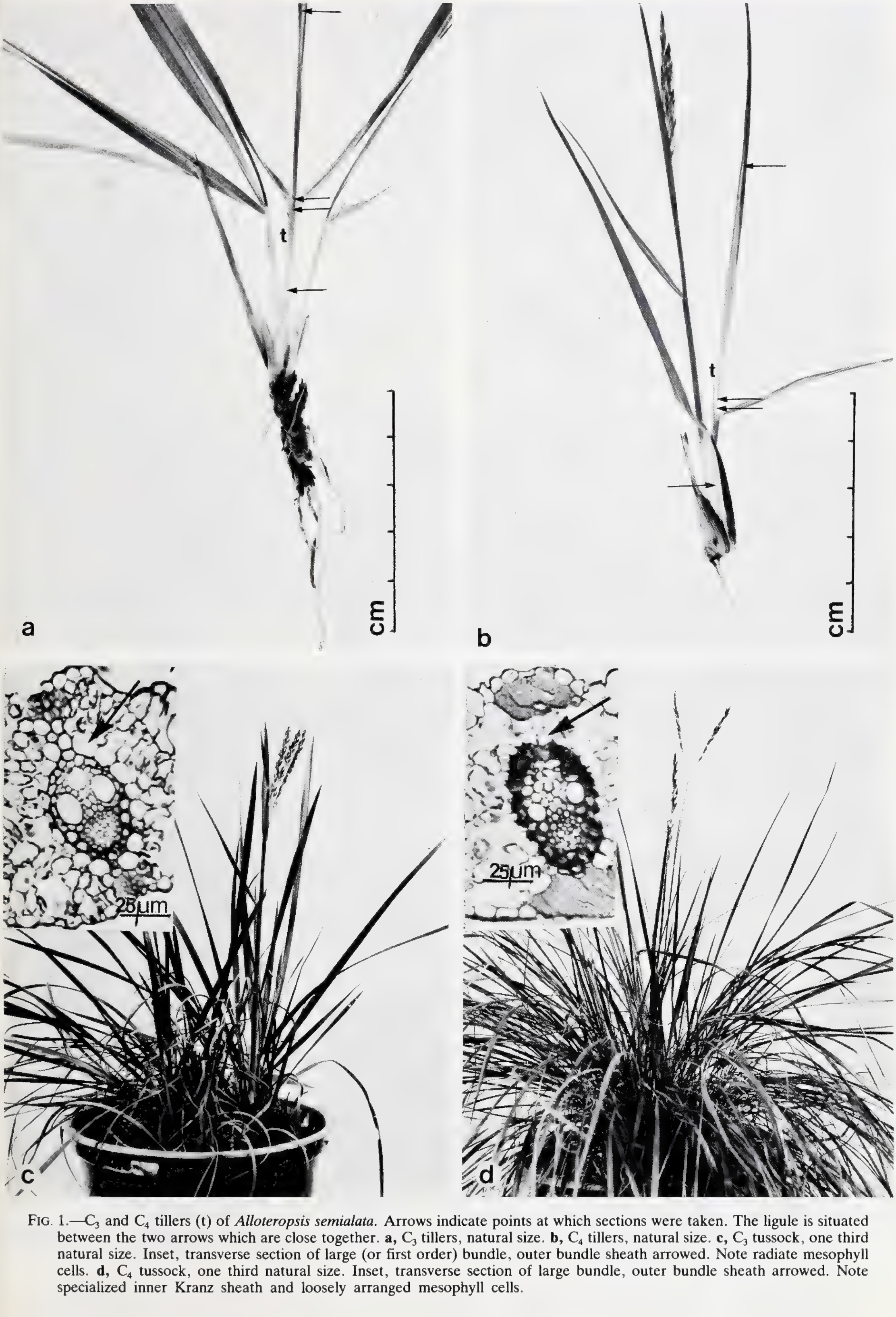
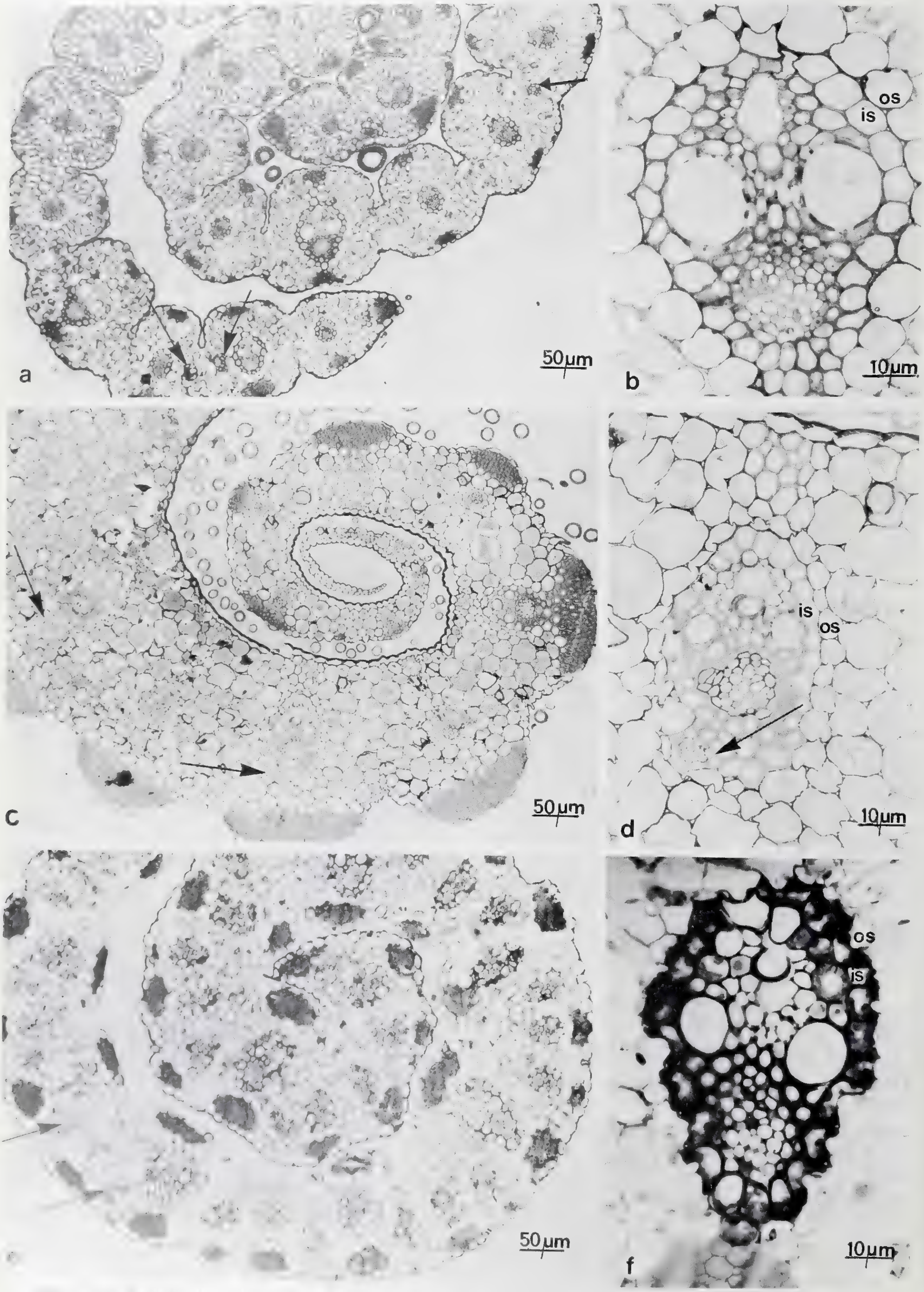


FIG. 1.—C_3 and C_4 tillers (t) of *Alloteropsis semialata.* Arrows indicate points at which sections were taken. The ligule is situated between the two arrows which are close together. **a,** C_3 tillers, natural size. **b,** C_4 tillers, natural size. **c,** C_3 tussock, one third natural size. Inset, transverse section of large (or first order) bundle, outer bundle sheath arrowed. Note radiate mesophyll cells. **d,** C_4 tussock, one third natural size. Inset, transverse section of large bundle, outer bundle sheath arrowed. Note specialized inner Kranz sheath and loosely arranged mesophyll cells.



[illegible] sections of C_3 and C_4 leaves. C_3: **a,** ligule region (pale green). Newly formed bundles [illegible] region. is = inner (mestome) sheath; os = outer sheath. C_4: **c,** mid-sheath. Newly [illegible]) bundle in mid-sheath. Note new bundle (arrowed); is = inner sheath; os = outer [illegible] bundles arrowed. f, large (first order) bundle in ligule region; is = inner (mestome) indicated. Fig. 1c, d show respectively the differing growth habit of C_3 pubescent and C_4 glabrous forms of *A. semialata,* with the related non-Kranz and Kranz anatomy

Light microscopy

Fig. 2a, b show typical vascular bundle sheath structure of the C_3 leaf, regardless of where sections are taken. There is a double bundle sheath, with an inner mestome sheath of small thickwalled cells and an outer sheath of parenchymatous cells.

At the light microscope level there is not much visible cell-content in either layer. Bundle sheaths of the C_3 leaf are similar in appearance regardless of whether they occur in the colourless leaf sheath, the pale green ligule region, or at midlamina. They are also remarkably similar in appearance to the colourless mid-sheath bundles of the C_4 leaf (Fig. 2c, d) except that in the C_4 bundle the parenchyma sheath is less well defined. This similarity is noteworthy, since parts of the C_3 leaf, viz. lamina and ligule have been exposed to light, whereas the C_4 leaf sheath has not. Investigation of the C_4 ligule area, which has been light exposed (Fig. 2e, f) shows that the vascular bundle of the C_4 ligule now shows the thickwalled Kranz inner sheath packed with chloroplasts; the outer parenchyma sheath of small thin-walled cells is poorly defined (at light microscope level) and poorly populated with chloroplasts. (cf. Fig. 2b with Fig. 2d, f).

New bundles appear to be forming in all three leaves shown in Fig. 2a, c, e. These apparently form close to an established bundle (Fig. 2d) and then are separated from it by the formation of a new bundle sheath and the intervening mesophyll cells (Fig. 2a, e). Serial sections would confirm this method of formation. In the C_3 leaf new bundles form equidistant from ab- and adaxial surface. In the C_4 leaf the older bundles occupy a more central position in the leaf, while the newer bundles form close to the abaxial surface. Only the largest (first order) bundles show metaxylem vessels in both C_3 and C_4 leaves.

Electron microscopy

Leaf sheath (colourless)

In both C_3 and C_4 leaves, in the colourless leaf sheath tissue amyloplasts are present in mesophyll cells and in both inner and outer bundle sheath cells (Fig. 3a, b).

Amyloplasts are more numerous in the C_4 mesophyll cells than in the C_3. Amyloplasts of the mesophyll cells show starch grains which may be intensely osmiophilic. The reason for this intense staining is not known (Fig. 3d, e). The C_3 mesophyll cells contain fewer amyloplasts with smaller grains. Both C_3 and C_4 mesophyll cells show chloramyloplasts i.e. plastids which have starch grains but also contain stroma lamellae (Fig. 3d) and plastids with prolamellar bodies (Fig. 3c) These two plastid types

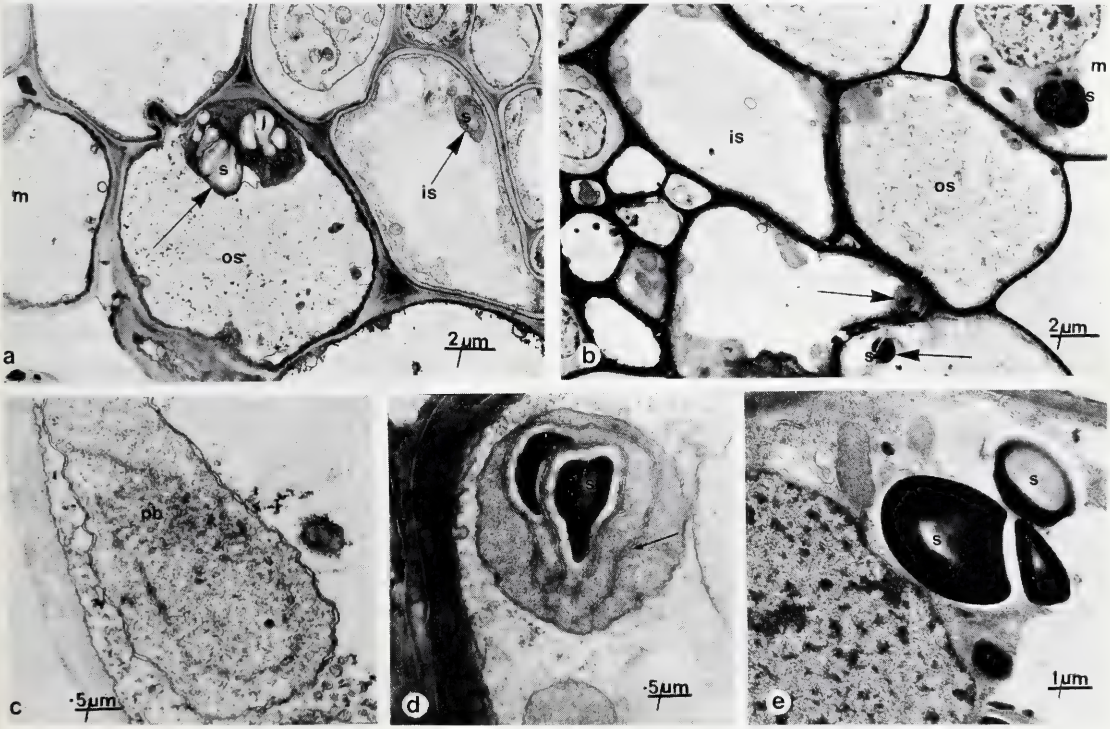


Fig. 3.—Tissue of the colourless leaf sheath. **a,** C_3 leaf sheath; inner (is) and outer (os) bundle sheath cells; amyloplasts (arrowed); m = mesophyll; s = starch. **b,** C_4 leaf sheath; inner (is) and outer (os) bundle sheath cells; amyloplasts (arrowed); m = mesophyll; s = starch. Note: amyloplasts are present in both inner and outer sheath (refer Fig. 2d). **c,** etioplast; pb = prolamella body. **d,** chloramyloplast containing starch grains (s) and lamellae (arrowed). **e,** amyloplast. Note osmiophilic starch grains (s).

more frequently seen in the C_3 mesophyll, while the C_4 mesophyll shows more amyloplasts. Average size of amyloplast profiles is 5 µm across.

Ligule region

All bundles regardless of size are surrounded by two sheaths in both C_3 and C_4 leaves (Fig. 4a, b). In the C_4 form the inner cells show enlargement and plastid proliferation in the form of numerous chloramyloplasts (Fig. 4e) and many etioplasts, a recognized stage in chloroplast formation (Fig. 4f).

Lamellae and lipid droplets are present in the stroma. Division figures are frequently seen (Fig. 4e). Due to their pleiomorphic shapes plastid profiles are difficult to measure, but are small averaging approximately 2 µm in length. In the C_4 leaf fewer plastids are seen in the parenchyma outer sheath than in the inner sheath. By comparison with the C_4 inner bundle sheath, there are also fewer plastids in the small cells of the C_3 inner bundle sheath (Fig. 4c, d). In the latter, plastids have more or less the same conformation as those in the C_4 inner sheath and are of similar small size. They show fewer division figures.

Midlamina (green)

At midlamina C_3 and C_4 leaves are clearly very different in appearance. Compare Fig. 5a & b.

C_4 leaf

The Kranz of specialized inner bundle sheath cells is well defined (Fig. 5a). Bundle sheath cells are filled with large chloroplasts, profiles averaging from 5–7 µm in length and 5–6 µm in width. Bundle sheath chloroplasts have stacked grana, numerous starch grains and large lipid droplets (Fig. 6a). Chloroplasts show a tendency towards centrifugal arrangement within the cells but this is not obvious. The outer bundle sheath chloroplasts often show a disrupted appearance and/or reduction in size (Fig. 5a). The thickened cell wall shows numerous plasmodesmata (Fig. 5c) both between inner and outer sheath and between inner sheath and mesophyll cells.

Mesophyll cell chloroplasts are peripherally arranged. They compare favourably with bundle sheath cells with regard to starch and lipid content. Starch grains appear similar in size in bundle sheath and mesophyll cells and appear in comparable numbers in the mesophyll (Fig. 6b). There is a size difference in chloroplast profiles. The chief size difference is seen in profile width. They are of comparable length. Mesophyll chloroplast profiles measure approximately 5 µm in length and 3 µm in width.

C_3 leaf

Chloroplasts in the inner mestome sheath are reduced in size and in number. (Fig. 5b, d). Profiles

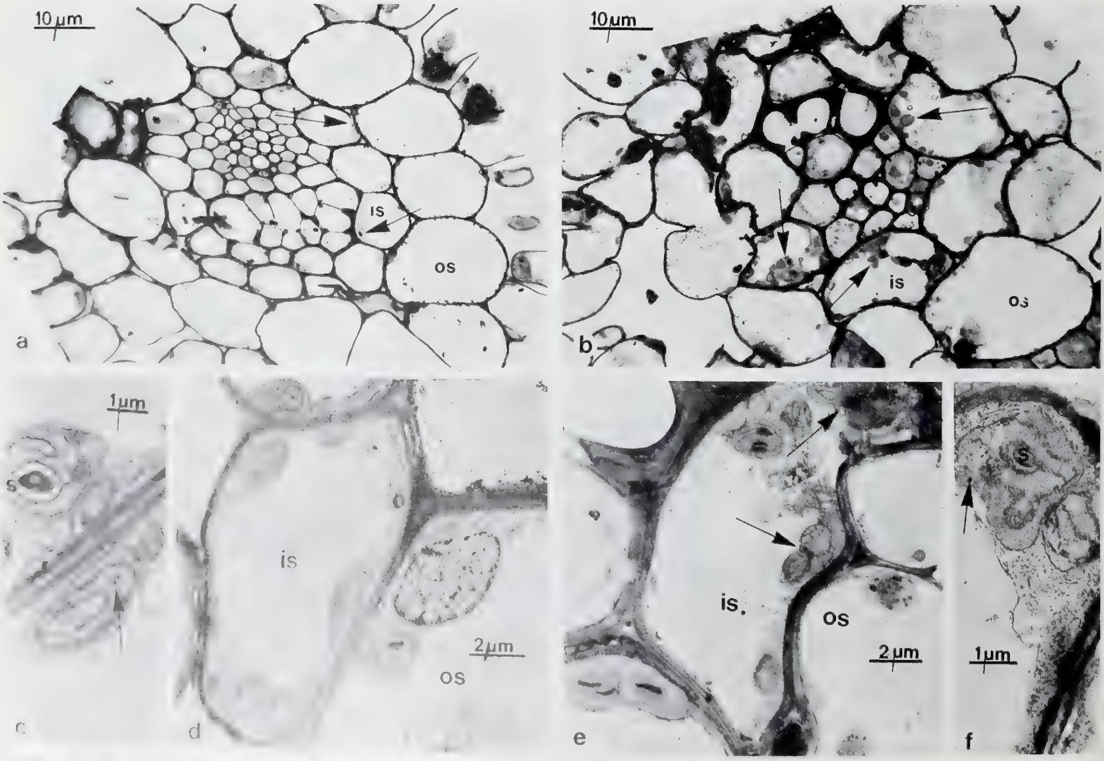


Fig. 4 — Tissue of the ligule region. a, C_3 leaf. Entire bundle; note that the inner sheath (is) contains few plastids (arrowed); os = outer sheath. b, C_4 leaf. Entire bundle; note plastid proliferation in inner or mestome sheath (is); os = outer sheath; plastids arrowed. c, C_3 leaf; chloramyloplasts in mesophyll cells. Lipid arrowed; s= starch. **d.** C_3 leaf inner (is) and outer (os) bundle sheath cells showing plastid population. e, C_4 leaf: inner (is) and outer (os) bundle sheath cells showing proliferating plastid population. Division profiles arrowed. f, C_4 leaf. Chloramyloplasts in mesophyll cells, lipid arrowed; s = starch.

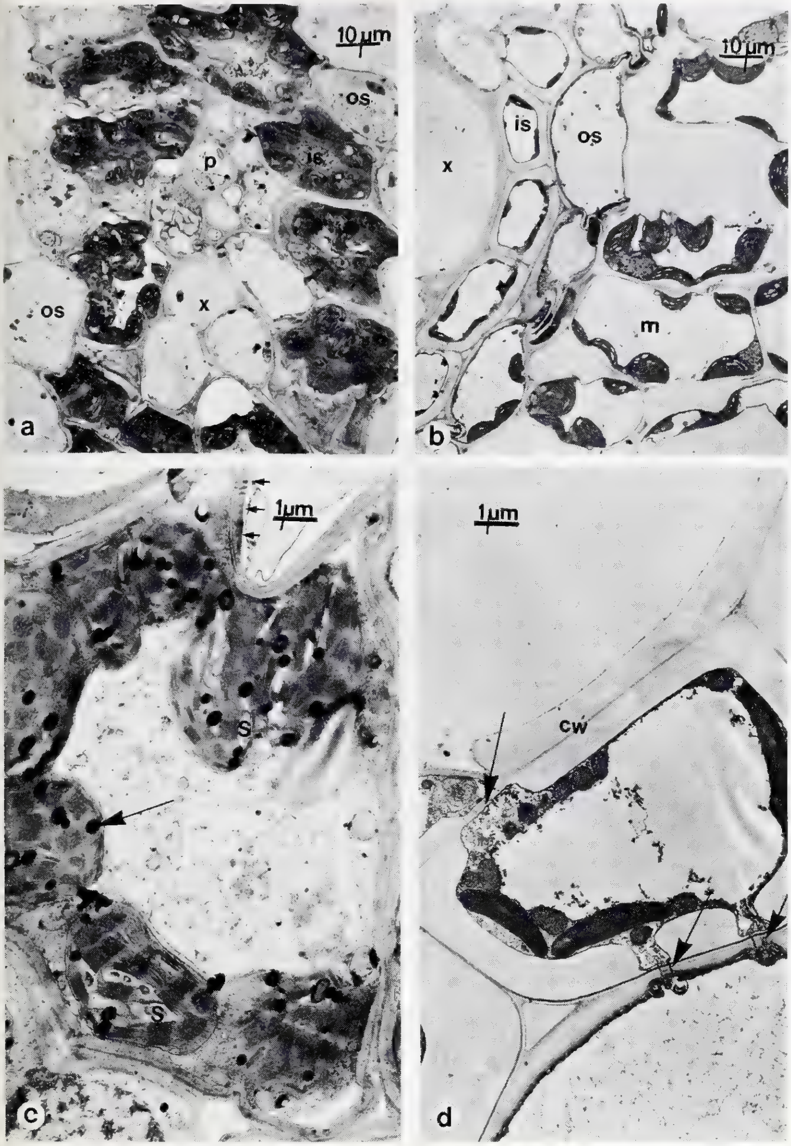


FIG. 5.—Tissue of the mid-lamina. **a,** C_4 leaf; entire bundle. Note the well-defined chloroplasts and the outer parenchymatous sheath (os) almost devoid of chloroplasts; p = phloem; x = xylem. **b,** C_3 leaf; portion of bundle. Note the small thick-walled mestome (inner) sheath (is) both with reduced peripheral chloroplasts; m = mesophyll; x = xylem. **c,** C_4 inner bundle sheath cell with large chloroplasts; plasmodesmata, small arrows; lipid, larger arrows; s = starch; **d,** C_3 inner bundle sheath cell with the thick-wall (cw) and reduced chloroplasts. Note plasmodesmata in embayments in wall (arrowed).

show marked reduction in width and length measuring approximately 1,5 µm across and 3–4 µm in length. They occupy a peripheral position in the cells which show very thick walls (Fig. 5d). Plasmodesmata are seen between inner and outer sheath cells and between inner sheath and vascular bundle. Where they occur the inner sheath wall is reduced in thickness forming embayments in the wall. Chloroplasts are virtually absent from the outer sheath.

Mesophyll cells show peripheral chloroplasts; they are characteristically lens-shaped (Fig. 6d). Profiles measure approximately 8 µm in length and from 2–3 µm across. They show stacked thylakoids, and numerous relatively small starch grains and lipid droplets (Fig. 6c, d).

Results of enzyme assays are shown in Table 1.

DISCUSSION

It is apparent from this study of chloroplast formation in *A. semialata* that ontogenetic studies require many different approaches. For this reason, points for discussion are dealt with under separate sections, viz ontogeny, taxonomy physiology and morphology.

Chloroplast and vascular bundle ontogeny

Four chloroplast types are present in *A. semialata:* mesophyll and specialized bundle sheath chloroplasts in the C_4 form and mesophyll and reduced bundle sheath chloroplasts in the C_3 form. All the chloroplasts present in the mature C_3 and C_4 leaves appear to be formed via an ontogenetic pathway similar to the one described by Hinchman (1972) in oat coleoptiles, as follows (Fig. 8): Amyloplasts are

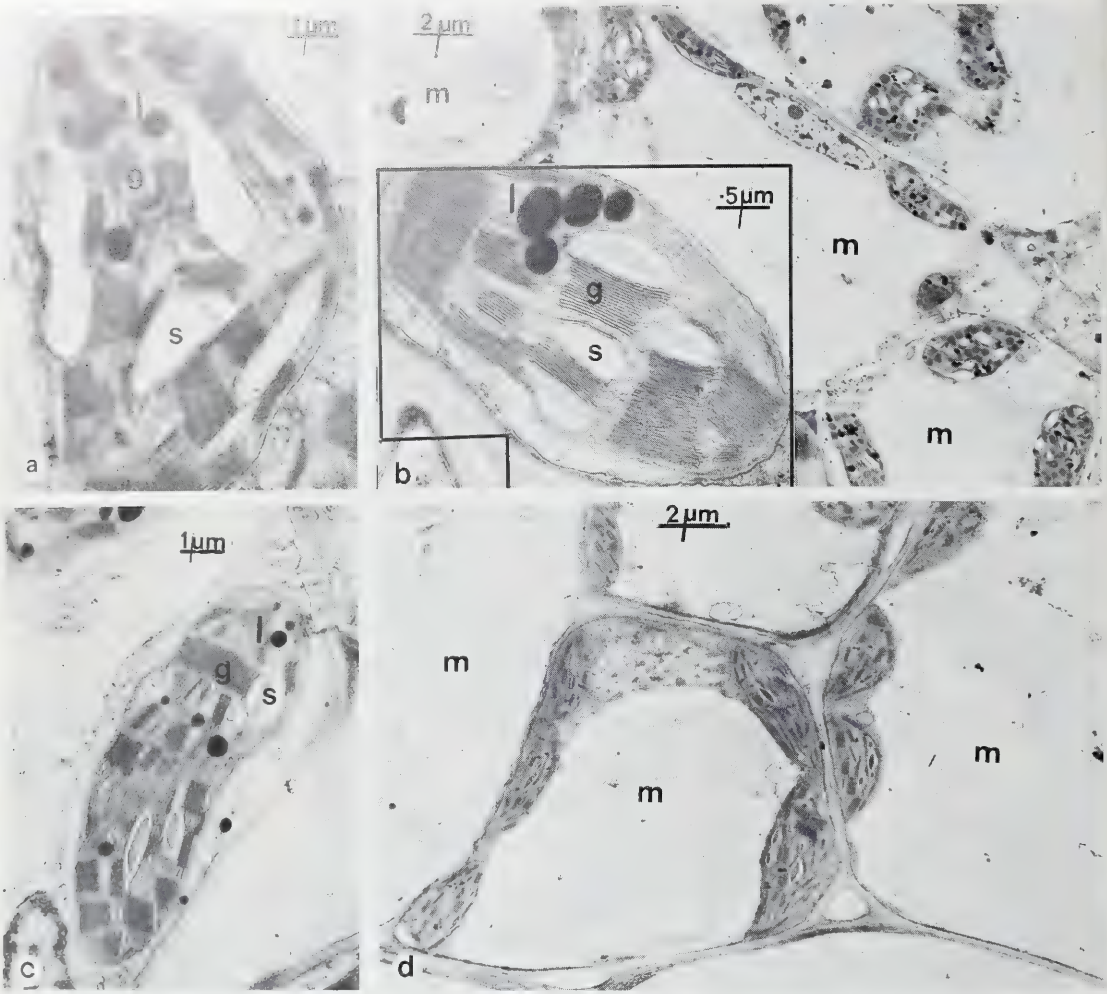


FIG. 6.—Mature chloroplasts in C_3 and C_4 leaves at midlamina. **a,** C_4 bundle sheath cell chloroplast. Well-stacked grana (g), large lipid droplets (l) and starch grains (s) are seen. Note absence of peripheral reticulum. **b,** C_4 mesophyll cells (m). Chloroplasts are peripherally arranged. Insert mesophyll chloroplast; g = grana; l = lipid; s = starch. **c,** C_3 mesophyll cell chloroplast with stacked grana (g) lens-shaped starch grains (s) and lipid droplets (l). **d,** C_3 mesophyll cells (m) with peripheral chloroplasts.

formed from proplastids in the coleoptile parenchyma. As the storage starch in the amyloplast is hydrolyzed, the amyloplast either reverts back to a 'permanent' proplastid with lamellae and ribosomes and no starch, (Fig. 8) or develops into a 'chloramyloplast', i.e. a plastid containing both lamellae and starch grains. This takes place in either the dark or the light. On exposure to light the chloramyloplast then either develops directly into a structurally mature chloroplast (Fig. 8a) or develops via an etioplast (Fig. 8b) which contains only unstacked lamellae and prolamellar bodies, into a chloroplast. Stages from amyloplast to chloramyloplast (Fig. 3c–e) are shown in both photosynthetic forms of *A. semialata*. In relating Hinchman's hypothesis to the current observations, it is proposed in this study that some proplastids are present in all the leaf cells whatever their age and position.

Hinchman (1972) established with buoyant density DNA studies that the plastid DNA component was identical irrespective of the plastid form, supporting his concept of a common origin for all plastids from the primary proplastid. The flow diagram of light related plastid ontogeny in the oat coleoptile (Hinchman, 1972) is interpreted in terms of plastid development in *A. semialata* (Fig. 8), which is light related in a normal growth situation.

The developmental sequence from proplastid to chloroplast on exposure to light is well known (Cran & Possingham, 1974; Engelbrecht & Weier, 1967). Stages shown in this investigation from amyloplast to chloroplast are less well known. These stages are important not only in chloroplast formation but also from the viewpoint of starch storage and translocation in grass leaves.

Vascular bundle ontogeny in the C_3 and C_4 forms of *A. semialata* has been traced by Frean & Cresswell (1981; see Fig. 7), who show provascular tissue in the lower leaf base and consider that *A. semialata* follows the general pattern of development

TABLE 1.—Activity of photosynthetic pathway enzymes extracted from *Alloteropsis semialata* plants grown inside and outside the greenhouse

Enzyme	μ moles NAD (P)/H or CO_2 mg Chl^{-1} min^{-1} Inside greenhouse temp. max = 28°C min = 10°C	Outside greenhouse temp. max = 16°C min = 4°C
NADP-malic enzyme	47,1	5,3
NAD-malic enzyme	1,4	0
NADP-malic dehydrogenase	4,8	2,1
NAD-malic dehydrogenase	143,9	192,9
PEP-carboxylase	37,5	50,4
Aspartate aminotransferase	22,5	283,9
Alanine aminotransferase	1,4	77,6
PEP-carboxykinase	0,1	7,8
RUBP-carboxylase	43,4	44,9

NADP = nicotinamide adenine dinucleotide phosphate.
NAD = nicotinamide adenine dinucleotide.
PEP = phosphoenolpyruvate.
RUBP = ribulose-1,5-bisphosphate.

as described in *Zea mays* (Kirk, 1971). In both these plants the youngest cells are near the base of the leaf and oldest near the tip. Leech, Rumsby & Thomson (1973) find that there is a progressive sequence of plastid differentiation from the base of the primordial leaf sheath to the lamina. It is difficult to relate this early plastid differentiation in the leaf base to formation of Kranz cells in the smallest (third order) bundles of the lamina. These small bundles arise chiefly in the lamina (but are also seen in leaf sheath and ligule extensions), whereas first and second order bundles form from the provascular tissue in the leaf base early in the development of the leaf in both forms of *A. semialata*. The increase in leaf breadth, is accompanied by an increase in number of third order bundles.

The formation of the third order bundles may be compared with the formation of the smallest bundles in the leaf of *Zea mays* (Sharman, 1942), where there is considered to be a 'double wave' of procambial (= provascular) differentiation, i.e. the first wave of differentiation proceeds from the base towards the tip in the early ontogenetic stages when the larger strands are formed. Then the next wave proceeds from the tip towards the base when the smallest bundles are formed together with the lateral anastomoses which are the last strands to appear. This appears to be the pattern of vascularization in *A. semialata* where the first and second order bundles correspond to Sharman's larger strands, and the third order bundles to his smallest bundles.

The formation of the small (third order) bundles can be explained on the basis of some proplastids being present in all the leaf cells. Cells and proplastids could become activated in delayed meristems (Esau, 1953) in the ground tissue to form the small bundles, in a second wave of vascular differentiation as described by Sharman (1942). More evidence is needed to prove this point. Autoradiographic labelling of a plastid component such as a nucleotide might provide an answer to this problem. Labelling in the presence or absence of specific inhibitors of chloroplast protein biosynthesis may assist in the elucidation of the rôle of the cytoplasmic genome and of the organelle in these aspects.

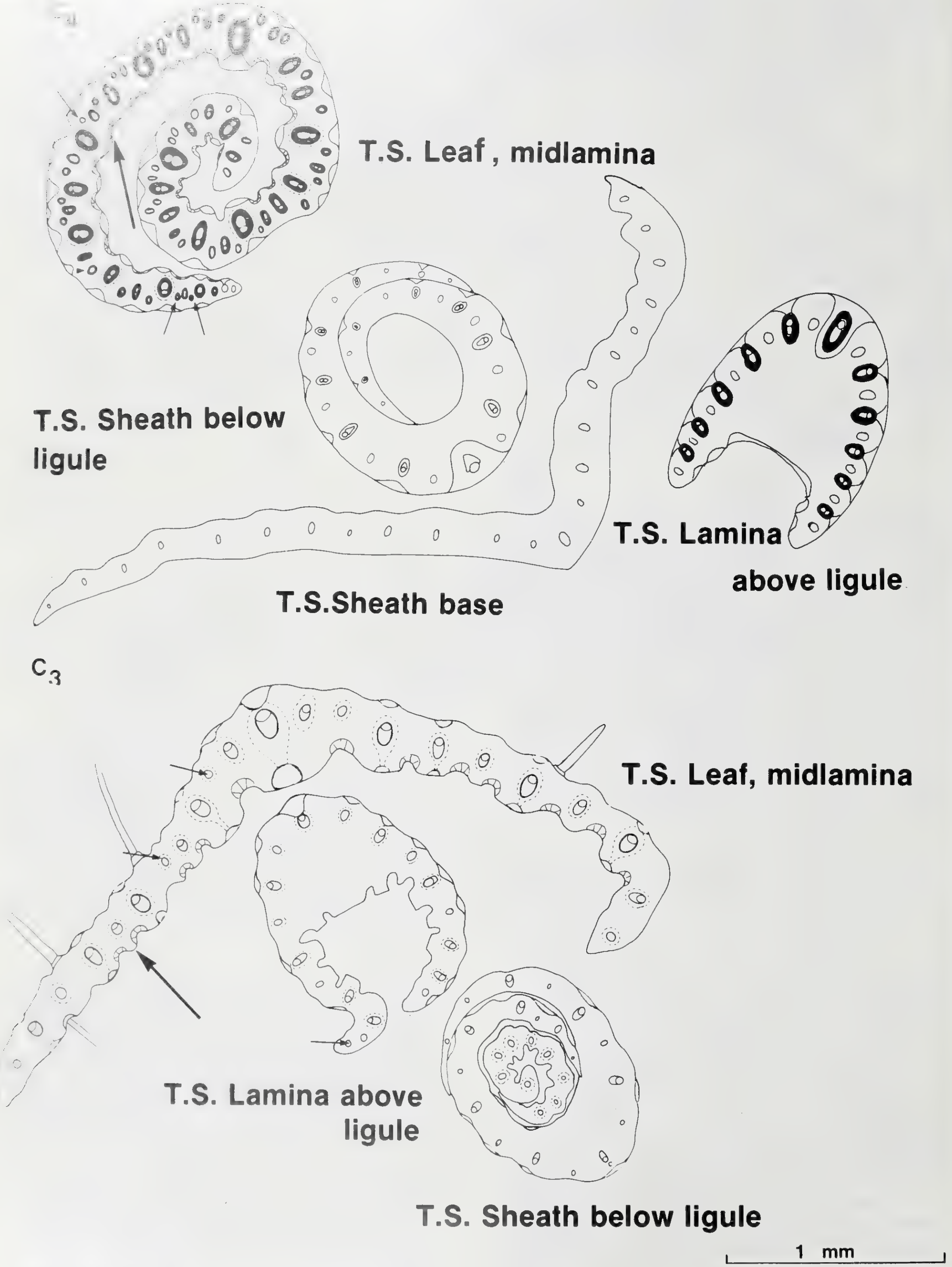
Chloroplast development in *A. semialata* indicates both cell determined and light influenced morphological changes in these semi-autonomous organelles; this is deduced from the fact that exposure to light results in the formation of Kranz sheath chloroplasts in the C_4 form only.

Laetsch & Price (1969) in following formation of dimorphic chloroplasts in sugar cane, leave unsolved the question of whether the structure of the chloroplast is programmed by the cell in which they occur, or whether they control their own development. If C_3 and C_4 forms of *A. semialata* are indeed controlled by one genome, an interesting new aspect has been added to the problem of chloroplast dimorphism which differs in C_3 and C_4 forms of *A. semialata*.

Brown (1975) points out that Kranz cells in most taxa are derived from the ground parenchyma, but that they can also be derived from procambium which develops into the vascular bundle, including the mestome sheath. Fig. 8 shows possible derivation of Kranz chloroplasts from the proplastids of vascular tissue. This derivation may apply to third order bundle formation as well as to formation of first and second order bundles.

Taxonomy

Brown (1975) proposes that all single-sheathed Panicoideae may have the Kranz sheath homologous with the mestome sheath. In those members of the Paniceae with both a mestome (inner) and a parenchymatous (outer) sheath, it is the parenchymatous sheath which is homologous with the Kranz sheath. Brown suggests that the single Kranz mestome sheath represents typical panicoid bundle sheath structure and that evolution of a Kranz sheath homologous with the mestome sheath indicates that in the Panicoideae there have been



[illegible] transverse sections of C_4 and C_3 leaves showing distribution of vascular bundles in leaf tissue. Note new bundles in [illegible] in both C_4 and C_3 leaves (small arrows). Xylem faces adaxial surface (large arrow). Modified from Frean & [illegible]

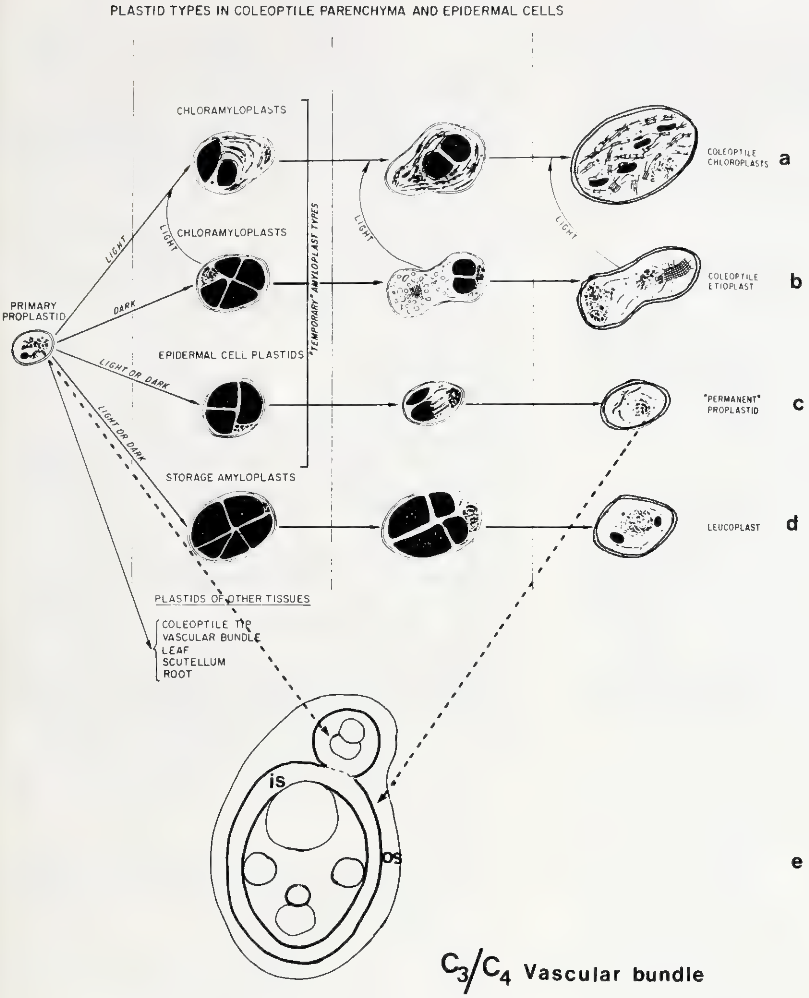


FIG. 8.—Flow diagram (modified from Hinchman, 1972) showing plastid ontogeny. **a,** from primary proplastid via amyloplast and chloramyloplast to chloroplast; **b,** from primary proplastid via amyloplast and etioplast to chloroplast; **c,** from primary proplastid via amyloplast to permanent proplastid; **d,** not followed in *A. semialata;* **e,** vascular bundle of C_3 or C_4 leaf showing possible derivation of plastids in inner (mestome) sheath from primary proplastids of the pro cambium and in the outer parenchyma sheath from permanent proplastids in the ground parenchyma.

two origins of Kranz tissue since some members have a Kranz parenchyma sheath and others a Kranz mestome sheath.

In the C_4 form of *A. semialata* in this study, not only are Kranz and mestome sheath homologous but there is a persistent parenchyma sheath almost devoid of chloroplasts. This is an unusual situation in the Poaceae generally and in the Panicoideae in particular. Brown (1975) notes three anatomical types in *A. semialata:*

1, non-Kranz in a South African specimen of the variety *ecklonii* (Stapf) Stapf similar to the C_3 form discussed in this study;

2, Kranz, with only one bundle sheath, homologous with the mestome sheath in an Australian specimen and

3, an intermediate anatomy as described in the C_4 form in this study, i.e. a Kranz mestome (inner) sheath, with parenchyma (outer) sheath cells smaller but still 'essentially empty' (and mesophyll cells not radially arranged).

Ellis (1974) describes this anatomy as representing an intermediate stage in the evolution of NADP-type anatomy. This matter is discussed in the following paragraphs.

Physiological anatomy

C_4 grasses, in which the primary product of CO_2 assimilation (oxaloacetate) is reduced to a high proportion of malate, are characterized by a single Kranz bundle sheath (Brown 1975; Hattersley & Watson, 1976; Ellis, 1977). Ultra-structurally the sheath cells surrounding the larger bundles are seen to have agranal chloroplasts with centrifugal arrangement and low mitochondrial frequency in contrast to grasses where a high proportion of oxaloacetate is aminated to aspartate, where there is a double bundle sheath with an inner or mestome sheath between the vascular tissue and the Kranz sheath.

This investigation using routine light and transmission electron microscope techniques, shows that the C_4 form of *A. semialata* does not conform anatomically to the single Kranz bundle sheath diagnostic for malate formers. The presence of grana in the Kranz sheath chloroplasts and the presence of large numbers of mitochondria in the bundle sheath cells, as well as the lack of definite centrifugal arrangement of chloroplasts, is not in agreement with the classification of this grass anatomically as an NADP-malic enzyme species, as suggested by Ellis (1977).

The presence of grana in the bundle sheath chloroplasts would place it into one of two non malate forming groups namely NAD-malic enzyme type or PEP-carboxykinase type; this is further supported by the presence of large numbers of Kranz sheath mitochondria and the presence of an outer parenchymatous bundle sheath.

Enzyme studies

Preliminary studies on the decarboxylating enzyme activities show that although the predominant activity is found to be NADP-malic enzyme, enzyme activity varies with temperature. It is lower in plants grown in the open (under winter conditions) than in plants kept in the greenhouse. There is a marked increase in PEP-carboxykinase with a decline in NADP-malic enzyme in the outdoor plants. Negligible activity of NAD-malic enzyme was found under either set of growth conditions.

It is noted that these results differ from those obtained by Frean, Ariovich & Cresswell (1980) where low levels of both NAD-malic and NADP-malic enzyme were found in C_4 plants grown at a temperature range of 16/30°C–20/30°C min./max.

It is concluded from this investigation that classification of C_4 grasses on the basis of anatomy and cytology is valid; but classification may become confusing if the different anatomical forms are given a biochemical nomenclature, particularly in view of the labile nature of any one particular decarboxylating enzyme with environmental changes.

Morphology

In the sample used in this investigation glabrous and pubescent morphologies were found to show, respectively, C_4 and C_3 anatomical and photosynthetic characteristics. However, the degree of pubescence is known to vary considerably in this widely distributed species (personal observations); no consistent morphological differences of sufficient significance have been found to warrant separation of the C_3 and C_4 forms taxonomically (Clayton, 1980: pers. comm.).

This investigation succeeds in its immediate aim in that it shows that plastid dimorphism exists in both C_3 and C_4 forms of *A. semialata* and that plastids become structurally distinguishable in young leaves on exposure to light only in those portions which are chlorenchymatous. However, no explanation of the resulting dimorphism can be given. Chloroplast and vascular bundle structure is related also to other aspects of the C_3/C_4 syndrome with

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Taxonomic status of the endemic South African bamboo, *Thamnocalamus tessellatus*

THOMAS R. SODERSTROM* and R. P. ELLIS**

ABSTRACT

Thamnocalamus tessellatus (Nees) Soderstrom & Ellis, [= *Arundinaria tessellata* (Nees) Munro] is the only endemic South African bamboo and occurs from the eastern districts of the Cape, through Lesotho and Natal, to the eastern Orange Free State at elevations of about 1 500–2 500 m. The Mountain Bamboo, or 'Bergbamboes' was first described by Nees in 1841 as a member of the genus *Nastus* because of the similarity, to him, of the spikelets between it and *N. barbonicus,* but was later transferred to the all-encompassing genus of the time, *Arundinaria,* the type species of which is endemic to the southeastern United States of America. Based on our present knowledge of bamboo genera, this South African species may be excluded from *Nastus* because the inflorescence is not a panicle but bracteate racemiform, the vegetative branches do not arise in a verticillate manner but are a series of subequal branches that are borne in a row above the nodal line and *T. tessellatus* has an androecium of three stamens and not six as in *Nastus.* The Bergbamboes, with sympodial rhizomes and branch complement of several subequal branches, can also not be maintained in *Arundinaria,* for monopodial rhizomes and a single branch at the node are typical of this genus. The simple, ebracteate, and exserted inflorescence of *Arundinaria* is also quite distinct from that of the Bergbamboes.

In order to place the South African bamboo more precisely we have made comparative studies of its leaf anatomy and epidermis, gross morphology, and analyses of its inflorescence and spikelets. The results of all these studies reveal a striking resemblance to members of the Sino-Himalayan genus, *Thamnocalamus,* to which we have accordingly transferred the species. The results are presented, together with an interpretation of the phylogenetic position of the Bergbamboes and possible events that led to the disjunction of species in the genus.

RÉSUMÉ

STATUT TAXONOMIQUE DU BAMBOU ENDÉMIQUE SUD-AFRICAIN, THAMNOCALAMUS TESSELLATUS

Thamnocalamus tessellatus *(Nees) Soderstrom & Ellis, [=* Arundinaria tessellata *(Nees) Munro] est le seul bambou endémique d'Afrique du Sud et il s'observe depuis les districts orientaux du Cap, à travers le Lesotho et le Natal, jusqu'à l'Est de l'Etat Libre d'Orange, à des altitudes d'environ 1500–2500 m. Le 'Mountain Bamboo' ou 'Bergbamboes' a été décrit pour la première fois par Nees en 1841 comme un membre du genre* Nastus *a cause de la similitude, d'après lui, de ses épillets avec ceux de* N. barbonicus *mais il fut transféré plus tard dans le genre plus général, à ce moment,* d'Arundinaria, *dont l'espèce-type est endémique au Sud-Est des États-Unis d'Amérique. En se basant sur nos connaissances actuelles des genres de bambous, cette espèce sud-africaine peut être exclue de* Nastus *parce que l'inflorescence n'est pas une panicule mais racemiforme ave bractées les branches végétatives ne poussent pas de manière verticillée mais sont une série de branches subègales qui sont portées en une rangée au dessus de la ligne nodale et* T. tessellatus *a un androcée de 3 étamines et non 6 comme* Nastus. *Les 'Bergbamboes'; avec des rhizomes sympodiaux et une de plusieurs branches subégales, ne peuvent pas davantage être maintenus dans* Arundinaria *car des rhizomes monopodiaux et une branche unique au noeud sont typiques de ce genre. L'inflorescence simple, sons bractées et exserte est aussi bien distincte de celle des 'Bergbamboes.' En vue de situer la bambou sud-africain d'une manière plus précise, nous avons fait des études comparatives de son anatomie foliaire et de son épiderme, de sa morphologie générale et des analyses de ses inflorescences et épillets. Les résultats de ces études révèlent une ressemblance frappante avec les membres du genre Sino-Himalayen,* Thamnocalamus *dans lequel nous avons par conséquent transféré l'espèce. Les résultats sont présentés avec une interprétation de la position phylogénétique des 'Bergbamboes' et des circonstances possibles qui conduisirent à la disjonction des espèces dans le genre.*

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Fundamental features of modern inflorescence morphology

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ABSTRACT

Great diversity is found in inflorescences of angiosperms. According to Troll this is due to the variation of two types only: the polytelic and the monotelic type.

In the monotelic inflorescence, the apex of the inflorescence axis commonly ends with a terminal flower. This also applies to all the floral branches below the terminal flower. All of these branches, whether branched or not, proved to be homologous elements, and they are all referred to by the term 'paracladia' because these branches repeat the structure of the main axis of the flowering system.

Accordingly, their ramifications are called paracladia of the 2nd to nth order. Since by the presence of the paracladia the number of flowers in the flowering system is increased, they may be called 'enriching branches'. Consequently the whole area which produces the enriching branches may be designated as an 'enriching field'. In the lower part of the flowering shoot this zone is commonly preceded by a 'field of inhibition' within which the development of paracladia is inhibited more or less abruptly. The same zonation can be recognized in the individual paracladia if these are not reduced in any way. In perennials, the axillary buds at the base of the whole stem do not develop within the same season, but will give rise to the innovation shoots at the beginning of the following season. Therefore this area has to be distinguished as a 'field of innovation'.

The polytelic type of inflorescence probably has been derived repeatedly from the monotelic during the evolution of angiosperms by reduction of the terminal flower and specialization of the paracladia of the monotelic system. The distal elements are reduced to single lateral flowers or lateral cymes (partial florescences) which constitute elements of an apical system composed of lateral flowers. Instead of ending in a single flower, the floral axis thus terminates in a multi-flowered so-called polytelic 'florescence'. The lower lateral branches repeat the structure of the main stem by producing (indefinite) florescences themselves and therefore may be termed paracladia (of the polytelic system). As in monotelic inflorescences the area of paracladia — the 'enriching field' — can be preceded by a 'field of inhibition' and, in perennial plants, by a 'field of innovation'.

Though generally we may confirm that the inflorescences of all species investigated (about 20 000 from nearly all angiosperm families) proved to be variations of one of the two fundamental types, it sometimes needs morphological experience to apply Troll's system to woody plants of tropical regions. Difficulties may derive from prolepsis and syllepsis of the innovation shoots, prolification of the inflorescence axis and, abundantly, by the deficiency of clearly marked limits between sprouts growing in different seasons. In each of such cases, however, the homologous flower-bearing-elements can be identified by comparing their positions within the whole system of ramification.

RÉSUMÉ

ASPECTS FONDAMENTAUX DE LA MORPHOLOGIE MODERNE DE L'INFLORESCENCE

Une grande diversité existe dans les inflorescences des angiospermes. Suivant Troll, on ne le doit qu'à la variation de deux types: le type polytélique et le type monotélique.

Dans l'inflorescence monotélique, le sommet de l'axe de l'inflorescence porte généralement une fleur terminale. Ceci s'applique aussi à toutes les ramifications florales en dessous de la fleur terminale. Toutes ces ramifications, qu'elles soient elles-même ramifiées ou non, s'avèrent être des éléments homologues et on les définit toutes par le terme de 'paracladies' parce que ces ramifications reproduisent la structure de l'axe principal de l'inflorescence.

Par conséquent, leurs ramifications sont appelées paracladies du 2^{me} au n^{me} ordre. Comme la présence des paracladies engendre un accroissement du nombre de fleurs dans l'inflorescence, on peut les appeler 'ramifications enrichissantes'. Par conséquent, toute la zone qui produit des ramifications enrichissantes peut être désignée comme 'zone d'enrichissement'. Dans la partie inférieure du rameau floral, cette zone est généralement précédée par une 'zone d'inhibition' dans laquelle le développement des paracladies est plus ou moins brusquement inhibé. La même zonation peut être reconnue dans les paracladies individuelles si celles-ci ne sont réduites d'aucune façon. Chez les plantes vivaces, les bourgeons axillaires à la base de la tige ne se développent pas au cours de la même saison, mais ils donnent naissance à des innovations au début de la saison suivante. Cette zone doit donc être distinguée comme 'zone d'innovations'.

Le type d'inflorescence polytélique a probablement dérivé par paliers successifs du type monotélique durant l'évolution des angiospermes par réduction de la fleur terminale et spécialisation des paracladies du système monotélique. Les éléments distaux sont réduits à de simples fleurs latérales ou à des cymes latérales (florescences partielles) qui constituent les éléments d'un système apical composé de fleurs latérales. Au lieu de se terminer par une seule fleur, l'axe floral se termine donc en une 'florescence' multiflore appelée polytélique. Les ramifications latérales inférieures reproduisent la structure de la tige principale en produisant elles-mêmes des florescences (indéfinies) et on peut donc les appeler paracladies (du système polytélique). Comme dans les inflorescences monotéliques, la zone des paracladies — 'zone d'enrichissement' — peut être précédée par une 'zone d'inhibition' et, chez les plantes vivaces, par une 'zone d'innovations'.

Bien que généralement nous pouvons confirmer que les inflorescences de toutes les espèces examinées (environ 20 000 appartenant à presque toutes les familles d'angiospermes) se sont avérées être des variations de l'un des deux types fondamentaux, il est parfois nécessaire d'avoir une certaine expérience en morphologie pour appliquer le système de Troll aux plantes ligneuses des régions tropicales. Des difficultés peuvent provenir du développement prématuré ou non des innovations, de la prolification de l'axe de l'inflorescence et, bien souvent, par le manque de limites bien définies entre les pousses croissant en différentes saisons. Dans chacun de ces cas cependant, on peut identifier les éléments florifères homologues en comparant leurs positions au sein de l'entièreté du système de ramification.

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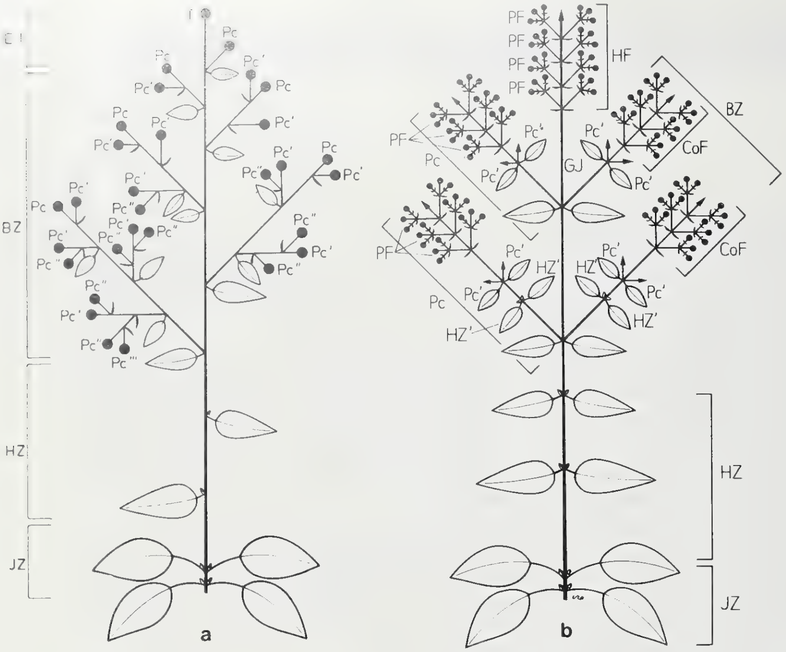

FIG. 1.—Diagrams of (a) a monotelic and (b) a polytelic inflorescence. T, terminal flower; Pc, paracladium; Pc', Pc'', paracladia of 2nd and 3rd order; HF, main-florescence ('Hauptfloreszenz'); CoF, co-florescence; PF, partial florescence; GJ, basal internode ('Grundinternodium'); EJ, final internode ('Endinternodium'); BZ, field of enrichment ('Bereicherungszone'); HZ, field of inhibition ('Hemmungszone'); JZ, field of innovation ('Innovationszone').

Correct interpretation of the morphology of inflorescences which reflects natural relationships must try to ascertain the flower-bearing elements which may legitimately be compared as identical structures. This, however, is connected with the elucidation of the structural plans of flowering plants. According to Troll (1955, 1964, 1969), the great diversity of inflorescences is due to the variation of two types only: the polytelic and the monotelic types.

In the *monotelic* inflorescence (Fig. 1a) the apex of the inflorescence axis commonly ends with a terminal flower. This also applies to all the floral branches below the terminal flower. All of these branches, whether branched or not, proved to be homologous elements, and they are all referred to by the term 'paracladia', because these branches repeat the structure of the main axis of the flowering system.* Accordingly, their ramifications are called paracladia of the 2nd to nth order. Since, by the presence of the paracladia, the number of flowers in the flowering systems is increased, they may be called 'enriching branches'. Consequently, the whole area which produces the enriching branches may be designated as an 'enriching field'. In the lower part of the flowering shoot this zone is commonly preceded by a 'field of inhibition' within which the development of paracladia is inhibited more or less abruptly. The same zonation can be recognized in the individual paracladia if these are not reduced in any way. In perennials the axillary buds at the base of the whole stem do not develop within the same season, but will give rise to innovation shoots at the beginning of the following season. Therefore, this area has to be distinguished as a 'field of innovation'.

In the *polytelic* type of inflorescence, which is no less frequent in angiosperms, there is no terminal flower at the summit of the primary axis. The shoot apex remains indefinite after developing a smaller or greater number of lateral flowers, the last of which often do not complete their development but atrophy in the same way as the end of the axis. This apical flowering system, which is composed of lateral flowers only, is a constant feature of this type of inflorescence and is now referred to by the special term 'florescence'. Instead of ending in a single flower, as in the monotelic inflorescence, the floral axis here terminates in a multiflowered so-called polytelic florescence.

If the lateral flowers composing the florescences are provided with prophylls, these may produce secondary flowers or sympodial flowering systems from their axils. When this is so, the florescence consists of cymose 'partial florescences' as for example in the inflorescences of most Scrophulariaceae and Labiatae (Fig. 1b). Within both families, this derivation is verified by many transitional forms.

Below the florescence terminating the main axis, there may be some branches which repeat the structure of the main stem by producing florescences themselves and which are therefore called 'paracladia' again. Their florescences are termed co-florescences, in order to distinguish them from the main florescence of the main axis. The apices of the co-florescences remain indefinite like those of the main-florescence.

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* [illegible] ladium (pl. paracladia) points to [illegible] inflorescences implies a regular [illegible] according to a certain order. To [illegible] rescences is a matter of symmetry [illegible] tical methods (Frijters, 1976; [illegible]

Within these polytelic synflorescences**, the same zonation can be observed as in monotelic flowering systems: a paracladial zone: 'enriching field' which precedes the main florescence, a 'field of inhibition' and, in perennials, a 'field of innovation'. The florescence is separated from the enriching field by a 'basal internode' ('Grundinternodium', Troll), which may be of remarkable length.

In both the monotelic and the polytelic types, the different elements may vary in many different quantitative respects according to the principle of variable proportions: in polytelic synflorescences, the main florescence may be extended, the number of its flowers may be increased in many different ways or, in other taxa, the main florescence may be reduced or even be missing altogether (truncate polytelic synflorescences). The paracladia, or any other part, may be well developed or reduced, their number may be increased, they may be missing or modified in different ways. The development of paracladia may be basitonic or acrotonic. Variations also exist in the diversity of phyllotaxis and foliation, shortening or lengthening of the internodes in different parts of the plant, different intensity and different modes of ramification and so on.

All species investigated to date (about 20 000 from nearly all angiosperm families) fit into the typological concept elaborated by Troll. Some problems, however, must still be investigated in more detail and some terminological questions must be discussed.

An essential difference between the types seems to be that in the inflorescences of the polytelic type the shoot apex of the inflorescence axis remains indeterminate. This, however, also occurs in some monotelic inflorescences in which the terminal flower aborts. In such truncate, monotelic synflorescences, however, the paracladia usually end in terminal flowers, thus revealing the monotelic character of the whole system.

The terminal flower of a monotelic system may be stunted or altogether missing, because the primordia of the uppermost paracladia 'comprise the whole of the apex, leaving no residuum to continue the growth of the axis'. This statement is made by Philipson (1947) for *Valeriana officinalis,* where the terminal flowers are missing in all paracladia of thyrsoid structure. As another example, *Linanthus liniflorus,* belonging to the Polemoniaceae, may be mentioned here. In this case, the terminal flowers are often more or less rudimentary.

In other examples, such as *Campanula rapunculoides* (Troll, 1969, p.286) or *Agrimonia eupatoria,* the development of the vigorous distal part of the inflorescence often takes a very long time and frequently remains incomplete, thus the terminal flower fails to develop on the main axis of the inflorescence. Terminal flowers, however, are produced in the paracladia, which are less vigorous. Examples like these command our attention, when we consider the aspect of inflorescence-evolution.

In many lianas and rosette geophytes, the growth of the main axis is indefinite. Therefore the main axis, though it may produce lateral flower bearing branches, never ends in a terminal flower. This may be demonstrated here by two closely related Rubiaceae, *Sabicea laxothyrsos* and *Bertiera letouzeyi.* The latter is a liana and, unlike *Sabicea,* it does not produce a terminal flower. Rosette geophytes with indefinite main axes are represented by many species of *Plantago,* by *Pleiocraterium plantaginifolium* (Rubiaceae) and the species of the genus *Phyllactis* (Valerianaceae). Here, the apex of the rosette changes periodically from the formation of absolutely sterile zones to the formation of fertile regions, in which thyrsoid 'partial inflorescences' originate from the axils of the rosette leaves. Later we shall return to this mode of growth commonly called 'proliferation'.

Comparing the two types of inflorescences, we conclude that the polytelic type is more highly evolved than the monotelic. There is much evidence that the polytelic type is derived from the monotelic by two steps of evolution:

1. reduction of the terminal flower and
2. specialization of the lateral branches, some of which are reduced to single lateral flowers or lateral cymes which constitute elements of the florescences, whereas the other branches are differentiated as paracladia (of the polytelic type!) which themselves form florescences.

This evolution has taken place in different taxa of the angiosperms, sometimes even in several groups of the same family, for example Rubiaceae (Weberling, 1977). Though both steps — reduction of the terminal flower and specialization of the lateral branches — may occur independently from each other, the pathway of evolution, usually indicated by transitional forms, is that of 'homogenization,' mostly combined with 'racemization' (Maresquelle, 1970; Sell, 1969, 1976) and then, 'truncation' or the reduction of the terminal flower.

The process of *homogenization* produces an increasing uniformity of the lateral branches within the distal parts of the flowering system which constitute the florescences in the polytelic synflorescences. Whereas, in monotelic synflorescences, the terminal flower usually blooms before the neighbouring laterals, now the sequence of flowering within the distal flower bearing parts is reversed. Finally, the efflorescence within the presumptive florescences follows the way of the initiation of the flowers, advancing from base to apex. The result of this process of *racemization* is that the last flowers often do not develop and at least the terminal flower is reduced. This is referred to as 'truncation' (Sell, 1969, 1976; see also Weberling, 1961, 1965; Troll & Weberling, 1966).

Following this argument, one can assume that the starting point of inflorescence-evolution must have been the (monotelic) panicle. By studying the primitive families of the Magnoliales (and Dilleniales), however, one finds only poor evidence for this assumption. The inflorescences of most taxa within these families are relatively highly derived by specialization into longshoots and flower bearing

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** synflorescence: a system of florescences or a system of a terminal flower and monotelic paracladia.

shortshoots or by proliferation. The polytelic type of inflorescence is not rare in these families. Therefore, it seems to be more advisable to accept the panicle as the 'central type' only, from which all the other forms of inflorescences can be derived. This does not necessarily imply a phylogenetical interpretation. Some previous authors, as Parkin (1914, p.559), pointed out that 'it seems highly probable that *flowers were originally* borne on *the plant singly, each terminal to a leafy shoot.'* We find such flowers in *Liriodendron,* many *Magnolia, Calycanthus* and others. These could as well represent a state close to the starting point of inflorescence-evolution (though we have to pay attention to the fact, that single flowers also 'may have arisen through the reduction of an inflorescence').

Pilger (1922, p.21) said: 'Die primitive Form des Blütenstandes der Angiospermen ist die 'beblätterte' Rispe; erst die Trennung von Laub-und Blütenzweigen resp. von solchen Jahresabschnitten führt zu einer schärferen Begrenzung der Blütenstände'. Translated, this means: The most primitive form of the inflorescence in angiosperms is the leafy panicle; only the separation of leafy and flowering branches respectively, of such seasonal shoots, leads to a more distinct delimitation of inflorescences.

This statement refers especially to woody plants. We must emphasize, however, that the zonation of a flowering system which has been described here for the inflorescences of both types applies equally to herbaceous and to woody plants. Nevertheless, in woody plants of tropical regions the delimitation of an inflorescence and consequently the identification of homologous elements may be difficult. This is largely due to the fact, that, in contrast to woody plants of the temperate and subtropical zones which develop distinct renewal shoots from the axils of the leaves below the terminal inflorescence, the synchronous (sylleptic) development and flowering of branches met with in many tropical trees and shrubs, sometimes leaves hardly any indication permitting determination of the position of a flower bearing system equivalent to that of other taxa.

The development of seasonal shoots, so characteristic for woody plants of the temperate zones, is often combined with a specialization between vegetative and flower producing shoots. This division of labour can also be observed in tropical woody plants and in some herbaceous plants *(Tussilago, Petasites).* In woody plants we often find a differentiation of the shoot system into long shoots and short shoots. Here, the production of flowers is limited to the short shoots situated in the axils of the long shoots, whereas the long shoots by their 'proliferating' growth contribute to the expansion of the whole branching system. In the temperate regions particularly, but not limited to them, the short shoots commonly develop and flower in the year that follows the development of the long shoot. Therefore, except in evergreen plants, at flowering time of the whole branch, the long shoot has already lost its leaves.

The problem of delimitation of comparable flower bearing parts may be explained by two examples, *Weigela* and *Symphoricarpos.* At first glance, a flowering branch of *Weigela* (Fig. 2a) might look like a polytelic synflorescence with an apical main florescence and lateral paracladia ending in co-florescences. We must, however, note that the foliation of the flower bearing branches as well as of the apical flowering system is preceded by a series of bud scales. On the other hand, the main branch of the whole flowering system has already lost its leaves. Our interpretation is, that we have to deal here with flower-bearing short shoots situated in terminal and lateral positions on a last year's long shoot. Each short shoot has to be regarded as a flowering system by itself. Results of comparative studies suggest that their inflorescences can be interpreted as much reduced, truncate, monotelic synflorescences with originally thyrsoid ramification.

In contrast, on a flowering branch of *Symphoricarpos rivularis* (Fig. 2b) we observe a leafy foliation throughout the whole branching system with the exception of the distal parts. Since all the flower-bearing branches are indefinite, the whole flowering system could be interpreted as a polytelic synflorescence with spike-like florescences (representing reduced thyrses). The lateral flowering systems, however, though blooming synchronously with the terminal inflorescence, are provided with one or several pairs of scale-like leaves at their bases, which actually function as bud scales for a short time. Therefore, we may assume that the lateral flower bearing shoots are short shoots which develop and flower without a preceding period of rest. This would not permit regarding them as paracladia of the same flowering system. The scale-like leaves, however, though temporarily functioning as bud scales, may also bear flowers in their axils. All this seems to indicate that we have to do with intermediate forms between a sylleptic branching system flowering more or less synchronously, and the differentiation into long shoots and (cataleptic) short shoots. Such transitional forms were found throughout the whole genus *Symphoricarpos.*

With regard to the typology of inflorescences which was explained before, we may confirm that the species of *Symphoricarpos* represent a state of transition between the monotelic and the polytelic type. These statements may be unsatisfactory for people who expect a definite assignment of all forms of inflorescences. We need to remember that the aim of comparative morphology is to elucidate relationships of forms and not to serve as pigeon-holes in which each organic form has its definite place.

In this sense, the application of the typological concept of Troll has already proved to be useful for the elucidation of morphological relationships and, hence, for the elucidation of systematic problems. This also applies to the inflorescences of the Caprifoliaceae which, at first, seem to be fundamentally different (Troll & Weberling, 1966).

Some confusion in the evaluation of flowering systems may also result from the proliferation of certain inflorescences. This peculiarity has been mentioned already in connection with the fact that the inflorescence axis may remain indefinite.

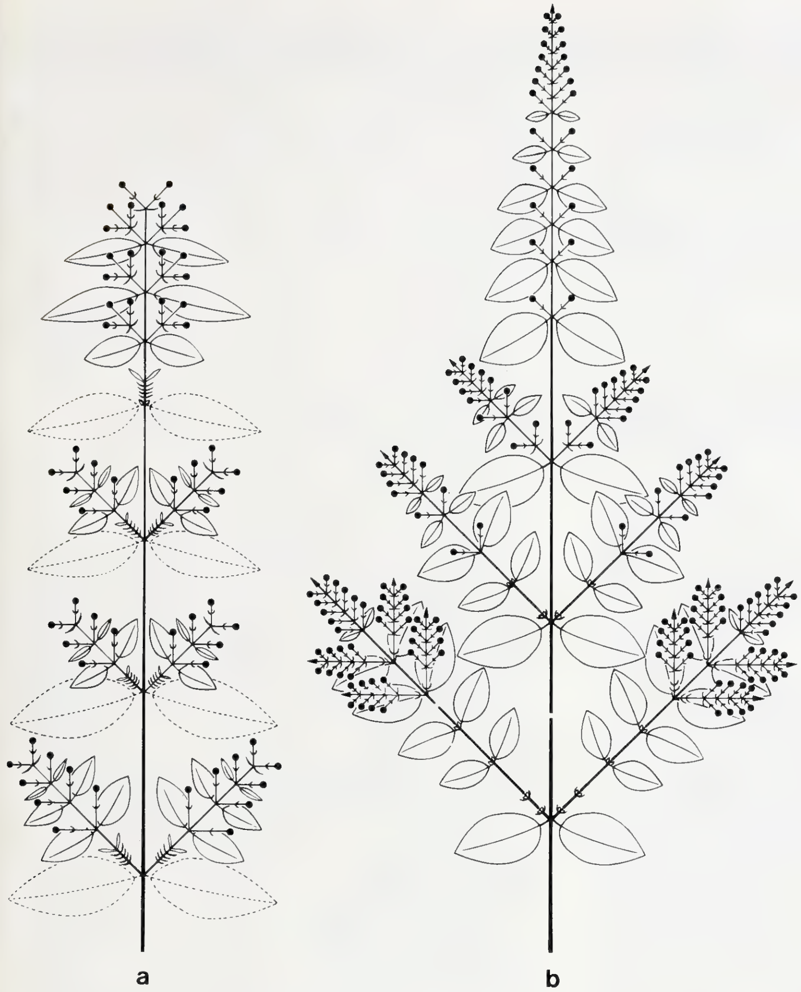

FIG. 2.—Diagrams of flowering branches of (a) *Weigela floribunda* (Sieb. & Zucc.) K. Koch and (b) *Symphoricarpos rivularis* Suksd.

Certainly, it does not seem advisable to refer the term 'proliferation' to the unlimited growth of any shoot bearing leafy branches which may, after further ramifications, finally produce flower-bearing elements. In the sense used by Troll (1959, p.116), it means a return of the inflorescence apex to vegetative growth. In *polytelic synflorescences* this may happen early, before the initiation of the main florescence: proliferation of the paracladial zone ('Frühprolifikation', Troll). As an example, *Lysimachia thyrsiflora,* may be mentioned here. Proliferation may also take place later when the apex of the main florescence reverts to vegetative growth: proliferation of the florescence ('Spätprolifikation', Troll). This applies, for instance, to *L. punctata* and *L. nummularia,* to *Eucomis punctata* and other monocotyledons. Proliferation may also occur in monotelic synflorescences (some species of *Campanula* and some Boraginaceae and Myrtaceae).

Parkin (1914, p.556) regarded proliferating inflorescences as a separate type of inflorescences, which he called *intercalary inflorescences,* because 'the flower-bearing part of the axis is . . . intercalated between two foliage-bearing portions'.

We must emphasize, however, that there are many taxa, *Veronica* and *Lysimachia* among others, which comprise both species with terminal bracteose and terminal foliose inflorescences and species with proliferating leafy inflorescences. Often these forms are connected by a continuous series of intermediate forms. At least, in these cases, we must regard these proliferating inflorescences as highly derived from terminal ones. This, in my opinion, also applies to woody plants.

Another problem is that of perennial inflorescences which we find, for example, in *Mitrophyllum grande* (Mesembryanthemaceae). The species, indeed the whole genus, is characterized by its heterophyllous, dimorphic or rather trimorphic foliation. Within each season the vegetative shoot develops only two pairs of leaves. The leaves of the primary pair are spreading, slightly flattened and have a short gamophyllous base. The leaves of the second pair, the 'mitre-leaves', are connate for the greater part of their length forming a double-pointed tube. The inflorescences, which are developed after many years of vegetative growth, are very simple. They only develop two prolonged internodes with one pair of bracts and end in a terminal flower. From the axils of the bracts secondary flowers may arise. They are provided with one pair of bracts. Their anthesis, however, is delayed until the next season. The same is repeated by the paracladia of the next order, which arise from the bracts of the preceding paracladia. They flower one after another with an interval of one season. Therefore, following Troll's interpretation, we have here a plurannual inflorescence. Troll regards this peculiarity as the antithesis of the successional innovation of certain plants (species of *Juncus, Asparagus* and *Canna indica*), in which several renewal shoots develop in a sympodial order within the same season.

According to Poppendieck (1976), in his monograph of the genus *Mitrophyllum,* the inflorescence is uniflorous. In his opinion, the secondary flowers which develop from the axils of the bracts are renewal shoots. He reports that species like *Mitrophyllum roseum,* the consecutive flowers are separated by vegetative parts with mitre-leaves (functioning as 'resting leaves', 'Ruheblattpaar'). In other species seasonal vegetative parts may be intercalated within the flower-bearing system. The question arises, however, as to whether the interpretation of these parts as renewal shoots is correct, considering the fact that the innovation of the vegetative parts proceeds from the axils of the basal, flattened leaves and consists of shoots producing flattened leaves and mitre-leaves in turn during a longer period. However, the solution of the question remains controversial. Plurannual inflorescences have not only been reported for Aizoaceae (Troll & Weberling, 1981), but also from some palms (Müller-Doblies, unpubl.) and some Chenopodiaceae (Urmi-König, unpubl.) and probably will be reported from other families too. We need to study them in more detail. Though the controversies mentioned here and other questions still open to discussion do not principally affect the typological concept elaborated by Troll, there still remains much research to be done.

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The ontogeny of the fruit and seed of *Momordica balsamina*

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ABSTRACT

The ontogeny and morphology of the seed and fruit of *Momordica balsamina* L. are discussed in detail and compared with some of the relevant literature. Cucurbitaceous ovules are usually described as anatropous but, according to this study, at least those of some taxa should be regarded as circinotropous.

RÉSUMÉ

L'ONTOGÉNIE DU FRUIT ET DE LA GRAINE DE MOMORDICA BALSAMINA

L'ontogénie et la morphologie de la graine et du fruit de Momordica balsamina *L. sont discutées en détail et comparées avec la littérature qui s'y rapporte. Les ovules des Cucurbitacées sont habituellement décrits comme anatropes mais, d'après cette étude, ceux de certains taxons au moins devraient être considérés comme circinotropes.*

INTRODUCTION

With 17 indigenous genera (Dyer, 1973) the family Cucurbitaceae is well represented in southern Africa. From the vast literature available on this family, it is clear that the fruit and seed morphology as well as seed physiology of these plants is very interesting, especially the behaviour of the so-called 'nucellar membrane' of which there is some disagreement concerning its interpretation. This study was undertaken to gain more knowledge about South African cucurbits and to clarify the placentation, origin of the aril and interpretation of the 'nucellar membrane'.

Momordica balsamina L. was chosen since plants were readily available in the botanical garden of the University of Pretoria. This plant is also of general interest as it has been used by local tribes for medicinal purposes (Watt & Breyer-Brandwijk, 1962). The plant is described by Meeuse (1962) as a perennial herbaceous climber, but in Pretoria the aerial parts are ephemeral and new branches are produced from the subterranean parts every year. Microsporogenesis and pollination were also studied but will be dealt with in another paper.

MATERIAL AND METHODS

The material used for this study was collected from plants growing in containers in the garden of the Department of Botany, University of Pretoria.

For the preparation of the semi-thin sections, female flower buds, pollinated flowers as well as young and mature fruits of different developmental stages, were dissected and fixed in 6% glutaraldehyde in 0,05 mol. dm^{-3} cacodylate buffer. The material was dehydrated and embedded in glycol methacrylate (GMA) according to Feder & O'Brien (1968). The monomer mixture used, was as described by Von Teichman und Logischen & Robbertse (1981). Sections of approximately 2 µm thick, were cut with glass knives on a Reichert OMU 3 ultramicrotome, stained with periodic acid-Schiff's reagent (PAS) (Feder & O'Brien, 1968) using 0,5% 2,4 dinitrophenol hydrazine (DNPH) in 15% acetic acid as a blocking agent. Sections were counterstained for 1–5 minutes in 0,05% toluidine blue in benzoate buffer at pH 4,4 (Sidman *et al.* 1961).

OBSERVATIONS

1. *Ovule development*

The inferior ovary of the female flower is tri-locular with three 'placental ridges' dividing each locule into two pseudo-locules (Fig. 1) In each pseudo-locule there are two pairs of circinotropous ovules. The basal parts of the ovules fuse, thus occluding the locules. Vascular supply to the ovules comes from one central vascular bundle in the distal parts of each of the placental ridges.

Ovule development starts with the initiation of the archesporial cell, which after a periclinal division, forms a parietal cell and a megaspore mother cell. The origin of the inner integument is dermal, whereas the outer integument is of subdermal origin (Fig. 2). The inner integument consists of only two cell layers and forms the micropyle (Figs 5 & 6), whereas the massive outer integument consists of approximately 10 cell layers.

The crassinucellus stems from repeated periclinal divisions of the parietal cell. A nucellar beak is partly formed by periclinal divisions of the nucellus epidermis (Figs 3 & 4). A nucellar canal, which is a very unusual structure, is formed between the megaspore mother cell and micropyle (see discussion).

The megaspore mother cell undergoes considerable elongation during the development of the nucellus (Figs 2 & 3). Since it is the chalazal megaspore that forms the 8-nucleate embryo sac, (Figs 4 & 6) the embryo sac can be regarded as being of the Polygonum type (Maheshwari, 1950).

The synergids are highly vacuolated cells with a very distinct filiform apparatus (Fig. 6), and the egg cell has a dense cytoplasm. The polar nuclei fuse before fertilization (Fig. 6c) and the antipodal cells become appressed in the chalazal end of the embryo

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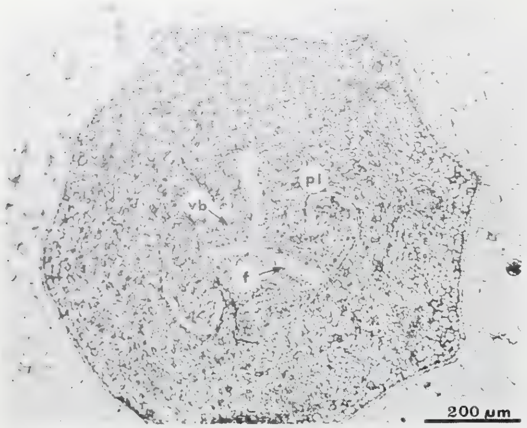

FIG. 1.—Transection of ovary showing three placental ridges. pl, placental ridge; vb, central vascular bundle; f, funicle.

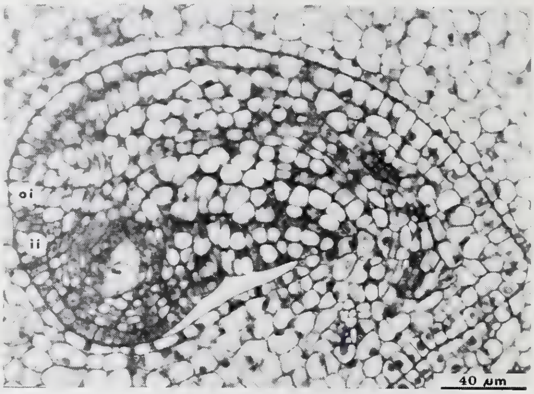

FIG. 2.—Longitudinal section of young ovule showing the megaspore mother cell and origin of the integuments. oi, outer integument; ii, inner integument.

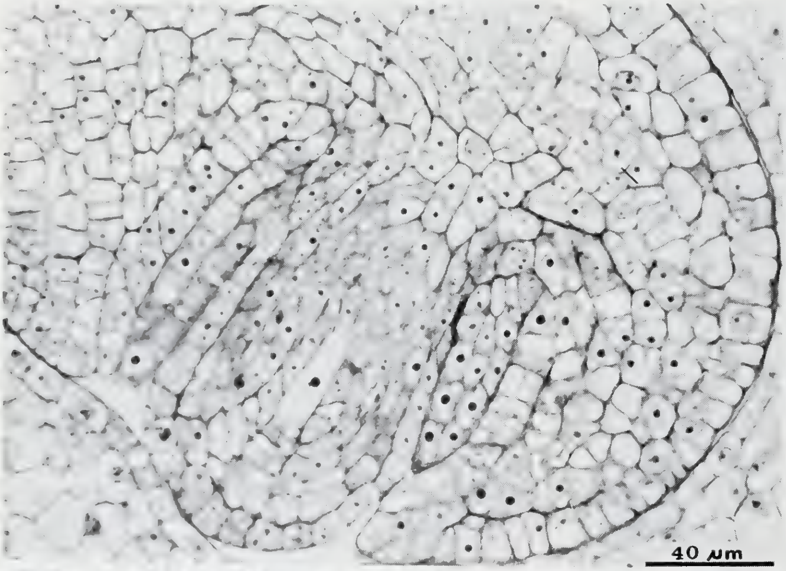

FIG. 3.—Longitudinal section of ovule showing elongated megaspore mother cell.

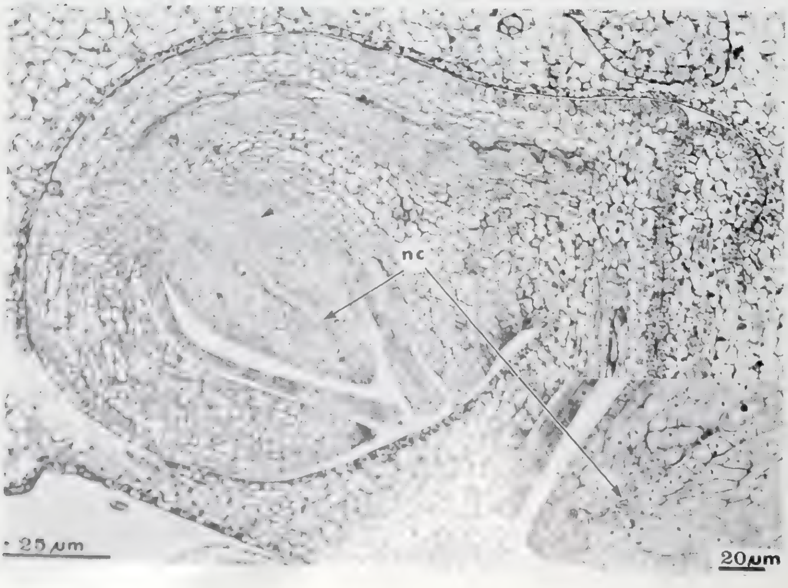

FIG. 4.—Longitudinal section of ovule showing nucellar canal in linear tetrad stage. nc, nucellar canal.

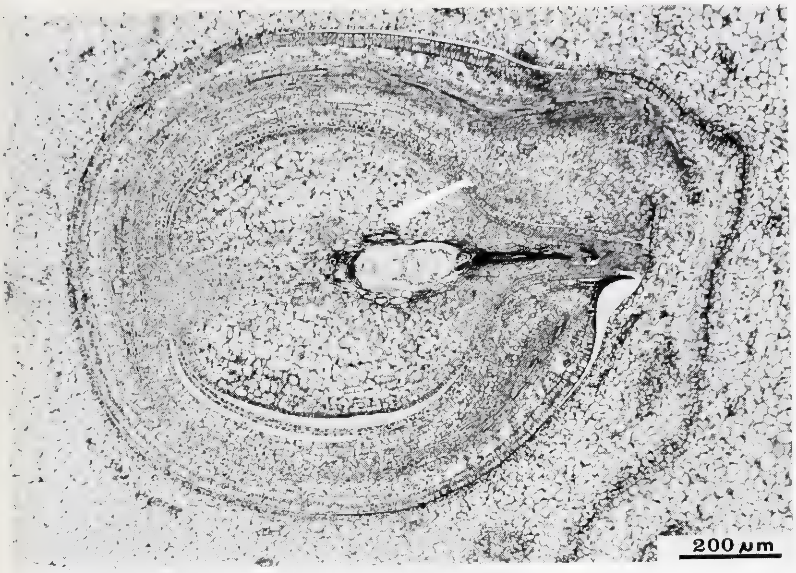

FIG. 5.—Longitudinal section of circinotropous ovule with thick-walled pollen tube in the nucellar beak.

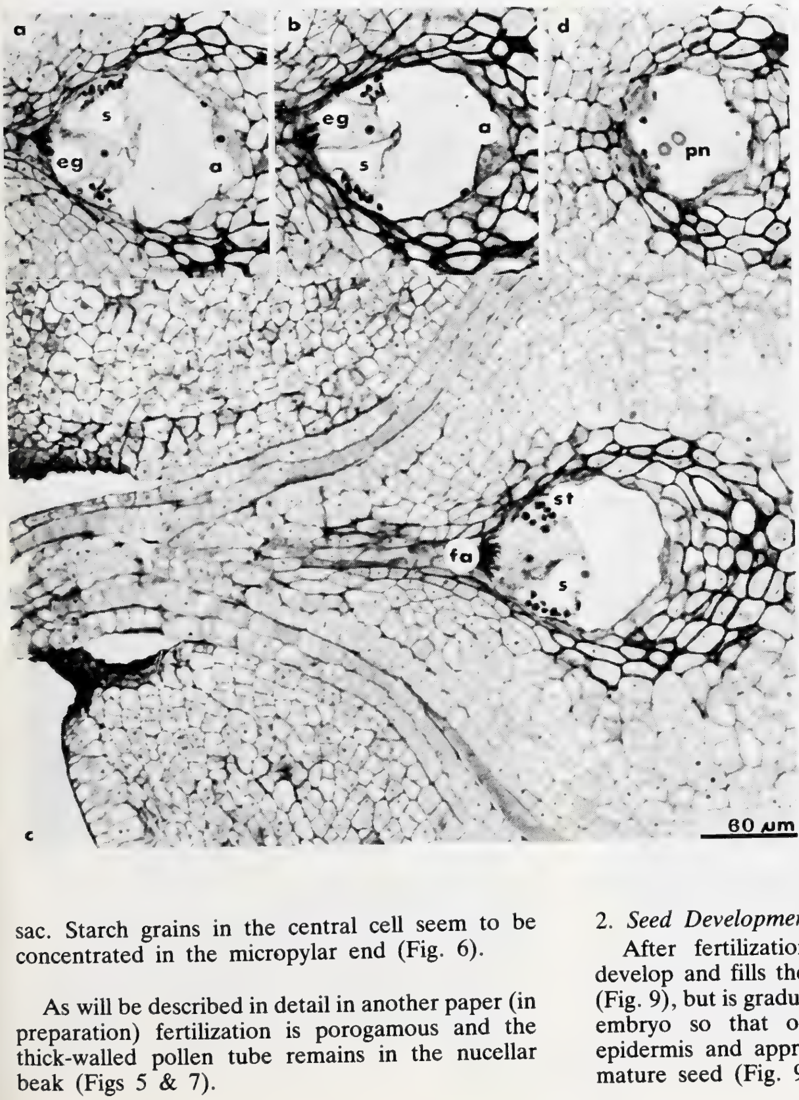

FIG. 6.—Series of sections of ovule showing: a, synergid (s), egg cell (ec) and antipodal (a); b, antipodals (a), synergids (s) and egg cell (ec); c, synergid (s), filiform apparatus (fa) and starch grains in central cells (st) and d, fused polar nuclei (pn).

sac. Starch grains in the central cell seem to be concentrated in the micropylar end (Fig. 6).

As will be described in detail in another paper (in preparation) fertilization is porogamous and the thick-walled pollen tube remains in the nucellar beak (Figs 5 & 7).

2. *Seed Development*

After fertilization, the nucellus continues to develop and fills the fullgrown but immature seed (Fig. 9), but is gradually absorbed by the developing embryo so that only the thick cuticle of the epidermis and appressed cell walls remain in the mature seed (Fig. 9).

The endosperm is of the nuclear type (Fig. 7), but initially it is limited to the micropylar end of the seed where it is confined to the embryo sac wall. No endosperm haustorium was seen. Although most of the endosperm is absorbed by the embryo, at least one layer of well defined cells remains and becomes attached to the outside of the embryo (Figs 8 & 10).

The inner integument remains two cell layers thick, but disintegrates in the maturing seed. The exotesta derives from the outer epidermis of the outer integument by repeated periclinal divisions (Figs 9 & 10). The outermost layer (e-layer according to Kratzer, 1918) consists of columnar cells with thick outer walls and thinner radial and inner walls, staining purple with toluidine blue (Sidman *et al.*, 1961). Below the e-layer are several layers of sclerenchymatous cells, staining greenish-blue with toluidine blue and representing the e″- and e′-layers of Kratzer (1918). Adjacent to the e-layer, cells of the e″-layer are small and globular, with a gradual transition to substellate or stellate cells with very thick walls. The e′-layer is ill-defined and consists of very thick-walled stellate cells.

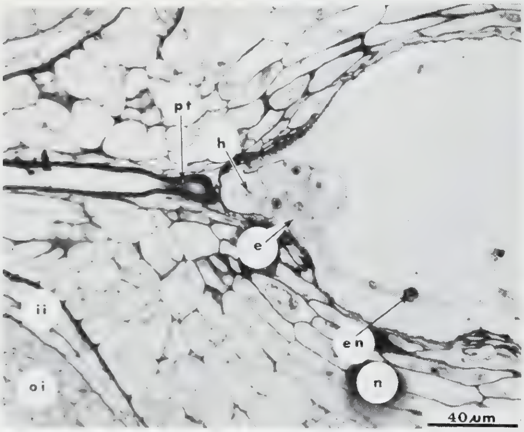

FIG. 7.—Section through a part of young seed showing onagrad-type embryo (e), hypophysis (h) and nuclear-type endosperm (en); pollen tube (pt); nucellus (n); inner integument (ii); outer integument (oi).

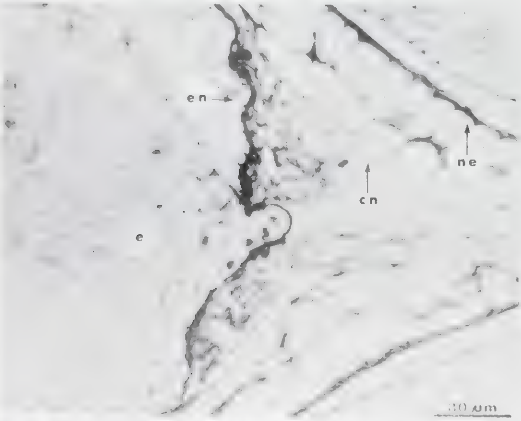

FIG. 8.—[illegible] immature seed showing [illegible] (ne), crushed nucellar walls [illegible] (en), and embryo

Three zones can be distinguished in the aerenchymatous endotesta. A zone comprising one to three layers of small, somewhat thick-walled cells is followed by a vascular bundle containing zone of much larger, thin-walled cells. The innermost zone consists of cells with a dense cytoplasm with lipid droplets around the nucleus (Fig. 10).

The embryo is of the onagrad-type (Foster & Gifford, 1974) with a very distinct hypophysis (Fig. 7).

3. *The fruit wall and pseudo-aril*

The fruit develops from an inferior ovary, but for the purpose of this description no distinction will be

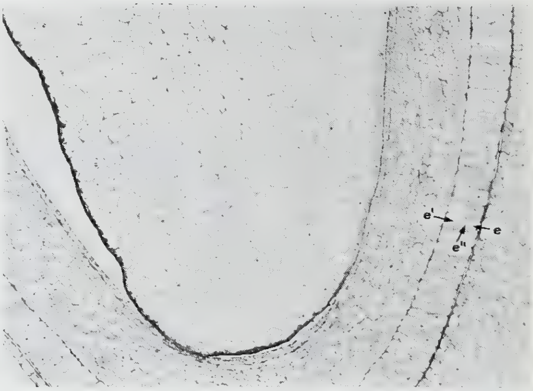

FIG. 9.—Transverse section of a fullgrown but immature seed showing formation of exotesta from outer epidermis of outer integument: e- layer; e′- layer and e″- layer.

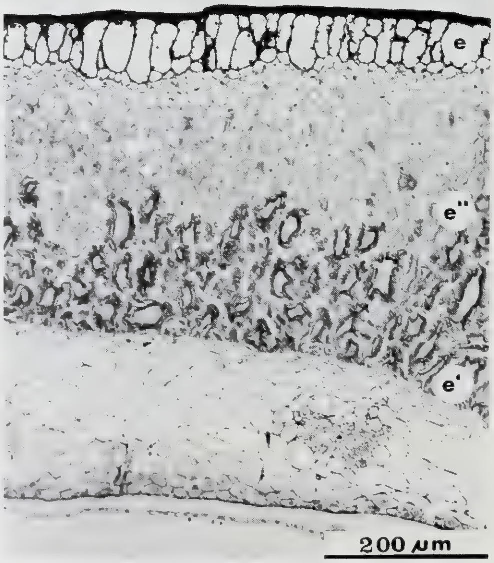

FIG. 10.—Transverse section of testa showing the different layers of the exostesta and endotesta (e- layer; e′- layer and e″- layer).

made between receptacle tissue and carpel tissue since, apart from cell size, it is very difficult to distinguish between these tissues. In the young fruit, six distinct zones are discernible: (1) outer epidermis, (2) hypodermis, (3) parenchymatous zone of large cells, (4) zone of radially elongated cells, (5) vascular bundle containing zone and (6) inner epidermis. The vascular tissue is found in the fifth layer, to the inside of the radially elongated cells (Fig. 11). At this stage placental tissue has merged with the funicles and endocarp, leaving each seed in a small cavity enveloped by an epidermis (referred to as zone 6 above).

In the maturing fruit, periclinal divisions of cells in the third zone causes its extension and shortening of the zones towards the inside (Fig. 12).

Autolysis causes the destruction of most of the cells in the fifth zone. Lysis starts from the inside of the fruit (Fig. 13), but the inner epidermis around the seeds as well as a number of adjacent starch containing cells (Fig. 15) are left intact and forms the pseudoaril. During the destruction of the fifth zone, the vascular tissue remains as loose strands in the mulch (Fig. 14).

In the ripe fruit, starch grains in the pseudoaril are hydrolyzed to sugars. Red chromoplasts are formed (see also Roderiquez *et al.*, 1976) resulting in a dark red, sweet tasting pseudo-aril around each seed (Figs 16 & 17). Ripe seeds are displayed after rupture of the fruits and recurving of the wall fragments.

DISCUSSION

According to Corner (1976), the ovules of the Cucurbitaceae are anatropous. We, however, interpret the ovules of *Momordica balsamina* as being circinotropous (Fahn, 1967). The reason for this difference in interpretation lies in differing interpretations of the anatomy of the fruit. Esau (1977) presents a diagram to explain her interpretation of the fruit of *Citrullus vulgaris*. In the diagram it is clearly shown that the three vascular bundles in the placentae derive from the fusion of the ventral bundles of adjacent carpels, but in the text she states: 'The margins of the carpels are incurved first centripetally and thus form the partitions between the locules. A second curvature carries the

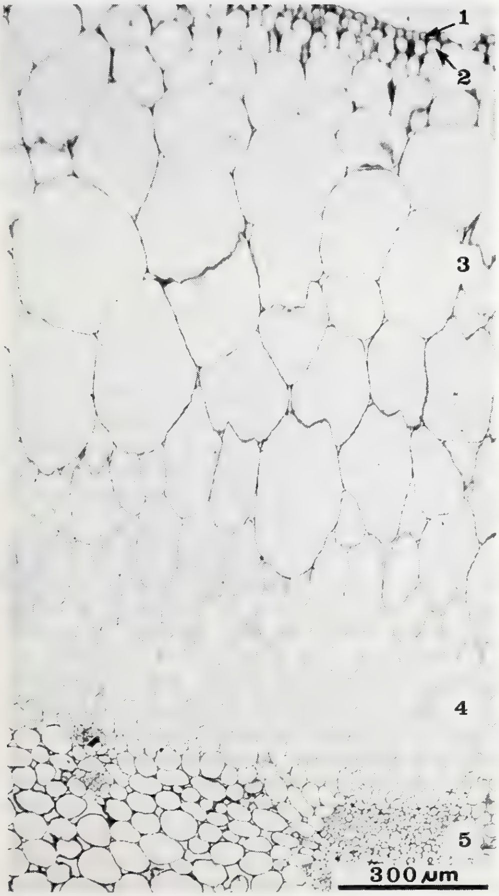

FIG. 11.—Transverse section of young fruit wall showing different zones (1–5).

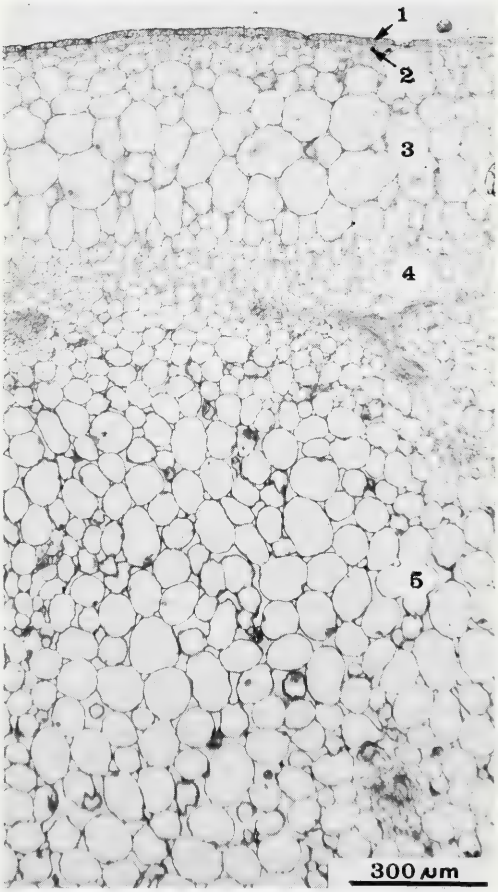

FIG. 12.—Transection of maturing fruit, showing different zones (1–5).

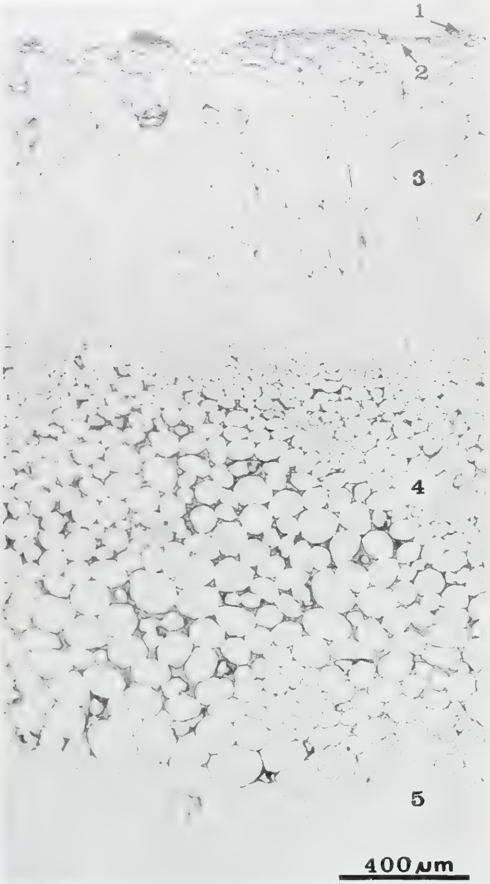

FIG. 13.—Transection of almost ripe fruit where lysis starts from the inside of the fruit.

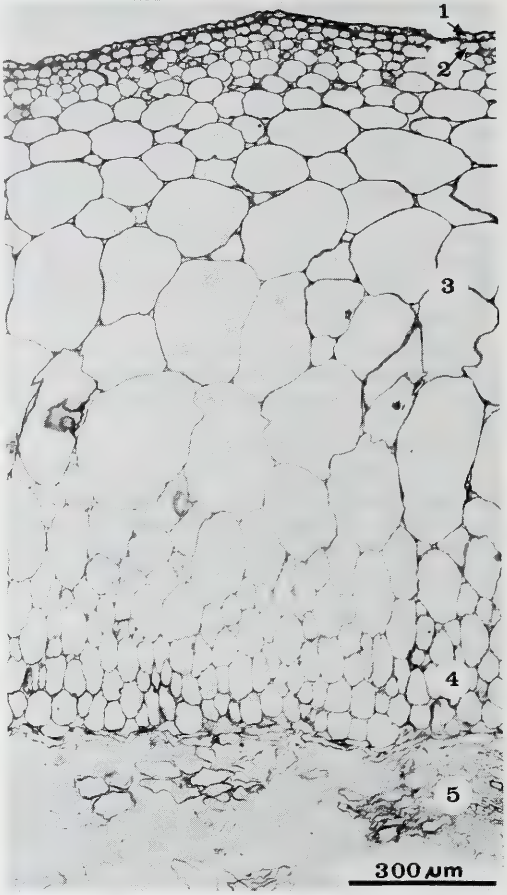

FIG. 14.—Transection of ripe fruit showing disintegrated 5th zone.

carpellary margins centrifugally so that each *locule* is divided'.

This interpretation conforms with that of Rendle and Judson as quoted by Puri (1954). Puri's own interpretation is that the placentation is parietal and that the 'Placental ridges are interpreted as "compound" structures, consisting partly of septal tissue and partly of placental tissue'. We cannot indulge in a lengthy discussion on the merits of these different interpretations. Whether the placental ridges are true septa or outgrowths of the parietal placentae, does not appear to affect our view that in *M. balsamina* the ovules can be interpreted as circinotropous. The reason for this view is that the centrifugal structures growing out from the point where the three central bundles are situated, are not continuous along the longitudinal axis of the ovary and must therefore be interpreted as the basal parts of the funicle (Figs 4 & 5). Consequently the funicle almost encircles the ovule, thus forming a circinotropous ovule. Circinotropous ovules are also found in the Cactaceae and Plumbaginaceae (Fahn, 1967). This might be of phylogenetic importance, since like the Cucurbitaceae, the Plumbaginaceae is one of the few exceptions where bitegmic seeds are found in the Sympetalae (Maheshwari, 1950).

The nucellar canal observed here is very unusual although, according to Kirkwood (1904), a similar canal has been observed by Amici (1842) in *Cucurbita pepo*. Schleiden (1944) rejected this observation by Amici but, as can be seen in Fig. 4, such a canal does exist at the stage where the linear tetrad has been formed.

In recent work on seed germination, mention is made of a 'nucellar membrane'. Mayer & Poljakoff-Mayber (1975), for instance, mention that 'Brown (1940) has shown that the nucellar membrane of *Cucurbita pepo* shows differential permeability to oxygen and carbon dioxide'. Brown (1940), however, refers to Höhnel's (1876) anatomical studies on membranes of the seed of *Cucurbita* where the latter author describes the 'inner membrane' as consisting of several layers, including remnants of the nucellar tissue as well as a layer of endosperm cells. In the mature seed of *M. balsamina* there is also a layer of cutinized epidermal walls of the nucellus, crushed nucellar walls and one layer of living endosperm left between the embryo and seed coat (Fig. 8) which conforms to Brown's (1940) concept of a 'nucellar

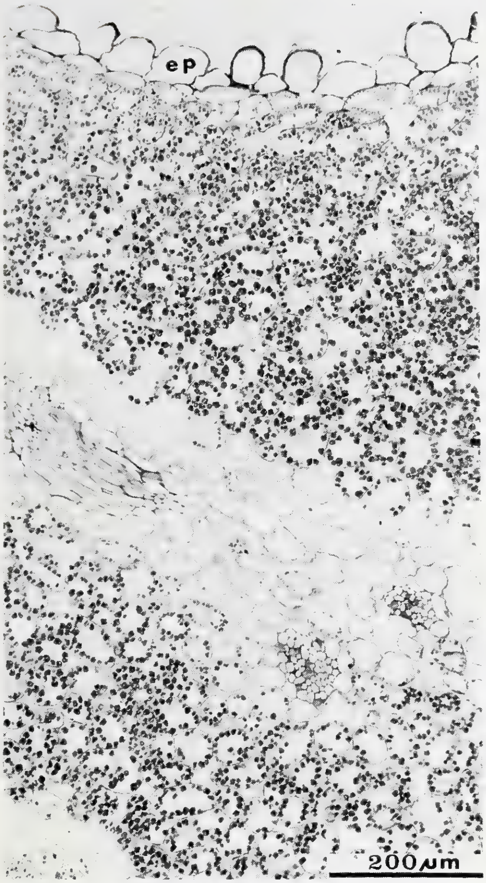

FIG. 15.—Section of maturing (light orange) pseudo-aril with starch containing cells. ep, epidermis facing seed.

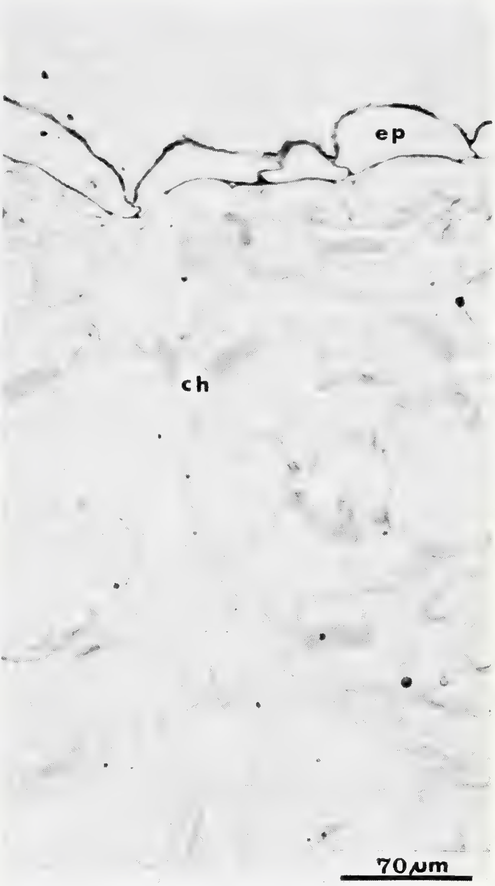

FIG. 16.—Section of mature (dark red) pseudo-aril where the starch grains have been hydrolised. ch, chromoplasts; ep, epidermis facing seed.

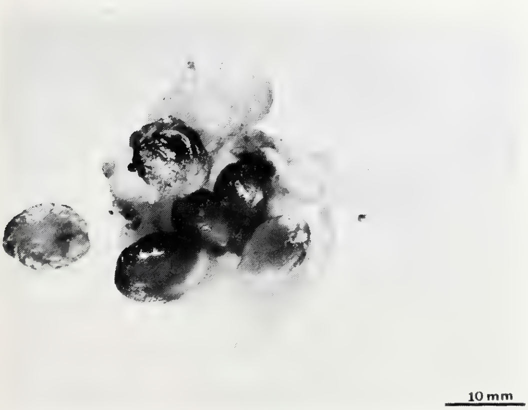

FIG. 17.—Ruptured fruit displaying ripe seeds each in a dark red pseudo-aril.

membrane'. This latter term should not be used since the remnants of the nucellus consist of appressed cell walls and the only living cells that could have any physiological influence on the seed are endosperm cells.

The outer wall layers in the ovary of *M. balsamina* conform to a great extent with those described by Kraus (1949) for *Bryonia dioica*. According to Corner (1976), the pseudoaril in *Momordica* derives from placental tissue but, as can be seen from Figs 2 & 5, the tissue adjacent to the seed on the antiraphe side is placental plus funicular, and that on the chalazal and rafe sides, of carpellary origin.

The broad, persistent pollen tube is mentioned by different authors e.g. Maheshwari, 1950 and Davis, 1966. Longo, according to Maheshwari (1950) and Kratzer (1918) believes that the pollen tube could have a haustorial function which seems possible if its contact with the suspensor in Fig. 7 is considered; however, more work is needed before an opinion can be formed.

The onagrad-type embryo of *M. balsamina* conforms with those of other Cucurbitaceae as described by Kirkwood (1904) and Davis (1966). No endosperm haustorium was seen (Chopra, 1955).

CONCLUSION

Seed morphology of *M. balsamina* differs very little from that of other investigated representatives of the Cucurbitaceae. As far as the placentation is concerned, we partly agree with the interpretation by Puri (1954). We differ from him, however, in regarding the centrifugal outgrowths, on which the ovules are borne, as part of the funicle with the implication that the ovules are interpreted as circinotropous.

Our interpretation of the 'false aril' (Corner, 1976) is that it is of heterogeneous origin, consisting of funicular, placental and carpellary tissue.

The term 'nucellar membrane' (Mayer & Poljakoff-Mayber, 1975) is misleading, since this membrane consists of a cutinized epidermal wall of nucellus, appressed cell walls of nucellar tissue and a layer of live endosperm cells adjacent to the embryo.

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Epidermis structure in Mesembryanthemaceae

H. -D. IHLENFELDT*

ABSTRACT

The Mesembryanthemaceae, which inhabit the deserts and semi-deserts of Southern Africa, exhibit two very different types of epidermis. The first is characterized by thick outer cell walls encrusted by oxalate crystals, a thick cuticle and thick wax layers. In the second type, the epidermal cells exhibit only very thin outer cell walls, not encrusted by oxalate crystals, a very thin cuticle, and wax layers are poorly developed; the most prominent feature of this type is the occurrence of huge idioblasts often protruding as 'bladder cells'. With regard to the climatic conditions in the native habitats this type of epidermis must be called 'abnormal'.

Both types of epidermis may form sculptures of three distinct size classes, which are not necessarily homologous. The function of these sculptures is still poorly understood. There is evidence that the sculptures influence the optical properties of the surfaces and thereby the radiation balance (and heat stress) of the leaves.

From recent research, it has become evident that the two different types of epidermis are the anatomical expression of two different strategies for survival under extreme conditions. Species with the idioblast type of epidermis exhibit a strategy that might be called 'opportunistic'. These species have developed a mechanism of gaining water from the atmosphere during the night under favourable conditions. There are indications that the idioblasts are involved in this mechanism.

RÉSUMÉ

STRUCTURE DE L'ÉPIDERME CHEZ LES MÉSEMBRYANTHÉMACÉES

Les Mésembryanthémacées qui habitent les déserts et semi-déserts de l'Afrique australe montrent deux types d'épiderme très différents. Le premier est caractérisé pas des cloisons cellulaires extérieures épaisses incrustées de cristaux d'oxalate, une épaisse cuticule et des couches épaisses de cire. Dans le second type, les cellules de l'épiderme montrent seulement des cloisons cellulaires extérieures très minces, non incrustées de cristaux d'oxalate, une très fine cuticle et des couches de cire pauvrement développées; le trait le plus saillant de ce type est la présence de grands idioblastes, souvent proéminents sous forme de cellules vésiculées. Par rapport aux conditions climatiques prévalant dans leur habitats d'origine ce type d'épiderme doit être appelé 'anormal'.

Les deux types d'épidermes peuvent former des sculptures de trois classes de taille distinctes, qui ne sont pas nécessairement homologues. La fonction de ces sculptures est encore mal connue. Il est prouvé que ces sculptures influencent les propriétés optiques des surfaces et de ce fait, l'équilibre de la radiation (et la tension de chaleur) des feuilles.

Des recherches récentes ont démontré que les deux types d'épidermes sont l'expression anatomique de deux stratégies différentes pour la survivance sous des conditions extrêmes. Les espèces avec le type d'épiderme à idioblastes montrent une stratégie que l'on peut qualifier 'd'opportuniste'. Ces espèces ont développé un mécanisme de captage d'eau de l'atmosphère durant la nuit dans des conditions favorables. Il existe des indications que les idioblastes sont impliqués dans ce mécanisme.

INTRODUCTION

The surface of a plant is the place where direct interactions between the plant body and the environment occur, and therefore plays an important role in the life strategies of land plants, especially with those plants that live under extreme climatic conditions. Consequently, features of the epidermis form an important part of character syndromes of plants such as xerophytes, e.g. the Mesembryanthemaceae, a well-known family of leaf succulent plants that inhabit the arid parts, deserts and semi-deserts, of Southern Africa.

EPIDERMAL STRUCTURE

Notwithstanding the fact that they all live in similar dry habitats, the Mesembryanthemaceae exhibit an enormous variety of epidermis types. Two distinct and quite different basic types of epidermis can be distinguished:

1. One type in which all 'ordinary' epidermal cells (except guard cells and subsidiary cells) are of nearly the same size. This type will be referred to as the 'xeromorphic type of epidermis' (Ihlenfeldt & Hartmann, 1982), as it exhibits clearly those characters assumed to be typical for the epidermis of a xerophyte (Fig. 1): reduced cell lumenae, caused by thick secondary wall layers, especially of the outer cell wall; encrustation by oxalate crystals; a cutinized wall layer and a cuticle proper of considerable thickness, and a wax layer covering the cuticle. Usually the stomata are sunken. Sunken stomata are thought to decrease residual stomatal transpiration by forming antestomatal chambers (Lyshede, 1979).

2. Another type which is characterized by the occurrence of much enlarged epidermal cells (idioblasts) among the 'ordinary' epidermal cells in a more or less distinct pattern (Fig. 2). These idioblasts normally protrude above the level of the 'ordinary' epidermal cells and have been called 'papillae' (Hagen, 1873; Oberstein, 1910) or 'bladder cells' (Öztig, 1940). This type of epidermis will be called the 'idioblast type of epidermis', a term

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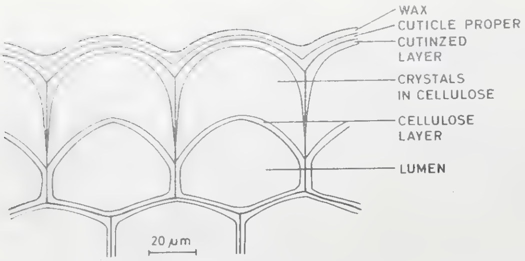
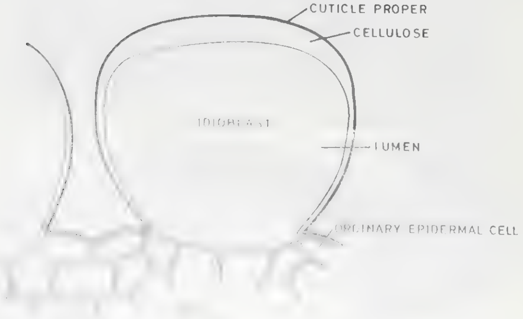


FIG. 1.—Xeromorphic type of epidermis with typical features.

derived from the most prominent feature of this type. The 'classical' xeromorphic features are not, or are very poorly, developed in this type. The outer cell wall of the epidermal cells remains thin, oxalate crystals are absent, a cutinized layer is not discernible and the cuticle is very thin (0,5 µm or less); wax is only poorly developed. This, however, does not apply to the idioblasts: in general their outer cell wall is 2−5 times thicker than that of the adjacent 'ordinary' epidermal cells, and a striking feature is that this outer cell wall is unevenly thickened, the greatest thickening found at the top of the idioblast. This special feature enables the idioblasts to change their shape to a certain degree: at times of water stress the idioblasts become flatter, their diameter increases. Consequently, if the idioblasts are of the protruding bladder type and densely crowded, the gaps between the idioblasts can become notably narrower; thus the narrow channels leading down to the stomata can be partially closed. The idioblasts exhibit further aberrant features: the outer cell wall can be encrusted by some oxalate crystals (observed by Öztig, 1940). The thin layer of cytoplasm has a foam-like appearance and contains chloroplasts and numerous mitochondria (Kramer, 1979), and in addition, some starch grains. Another notable feature is the occurrence of a certain number of pit-like cavities in the outer cell wall; these are concentrated in a zone just above the level of the 'ordinary' epidermal cells. Furthermore, the orientation of the apertures of the stomata is remarkable: the apertures are nearly always parallel to the outline of the adjacent idioblasts. Finally, in this type of epidermis, in contrast to the xeromorphic type, the stomata are never sunken.



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The great variety of epidermal types described in the literature for the Mesembryanthemaceae can be shown to be a combination of one of the two basic structural types of epidermis with different size classes of sculptures; the latter can be of different origin, i.e. they are not necessarily homologous.

The surface sculptures can be classified into three distinct size classes:

I. Surface sculptures of 0,15−1 mm and more in diameter, visible with the naked eye (Fig. 3.1−3.4).

II. Surface sculptures of 20−50 µm in diameter and 20−150 µm in length, being protuberances of epidermal cells (Fig. 4.5−4.6).

III. Surface sculptures of 1−10 µm in size, consisting of the wax cover (Fig. 3.5−3.6).

In the idioblast type of epidermis, sculptures of size class I are formed by the idioblasts reaching more than 2 mm in diameter in some extreme cases (Fig. 3.1 & 3.3). Sculptures of size class II can only be developed by the idioblasts (in contrast to the xeromorphic type of epidermis, see below) (Figs 4.5 and 5.1 & 5.3). These sculptures are protuberances of the idioblast cells, ranging from flat dome-like forms e.g. *Aptenia* N.E.Br. (Fig. 4.4) to hair-like papillae, single [e.g. *Jacobsenia hallii* L. Bol. (Fig. 4.5)] or paired [e.g. in the genus *Trichodiadema* Schwant. (Fig. 5.3)], and to branched structures resembling antlers [*Anisocalyx vaginatus* (L. Bol.) L. Bol. (Fig. 5.1)]. Sculptures of size class III are rare in the idioblast type of epidermis; they are represented by wax platelets that are orientated vertically [e.g. *Prenia sladeniana* (L. Bol.) L. Bol. (Fig. 3.5)] or by thread-like structures [in the genus *Malephora* N.E.Br. (Fig. 3.6)]. In contrast to sculptures of size class II, all cells of the epidermis are capable of producing these sculptures.

In the xeromorphic type of epidermis, sculptures of size class I are represented by local surface elevations, formed by groups of 'ordinary' epidermis cells and usually positioned above a huge tannin idioblast in the mesophyll below (Fig. 3.2 & 3.4). In these elevated areas stomata are absent (e.g. *Titanopsis* Schwant.). Sculptures of size class II are formed by papilla-like projections of the epidermal cells; all epidermal cells (excluding guard cells) are capable of forming papillae (Fig. 4.6), but sometimes papillate epidermal cells are restricted to elevated areas (e.g. *Odontophorus* N.E.Br.). Sculptures of size class III are formed by the wax cover as in the idioblast type of epidermis.

ECOLOGICAL SIGNIFICANCE OF THE EPIDERMAL STRUCTURES

Obviously the complicated epidermal structures described are of ecological significance. This can be inferred from the fact that a relatively large amount of material produced by photosynthesis (strongly inhibited by the deficiency of water, which is the

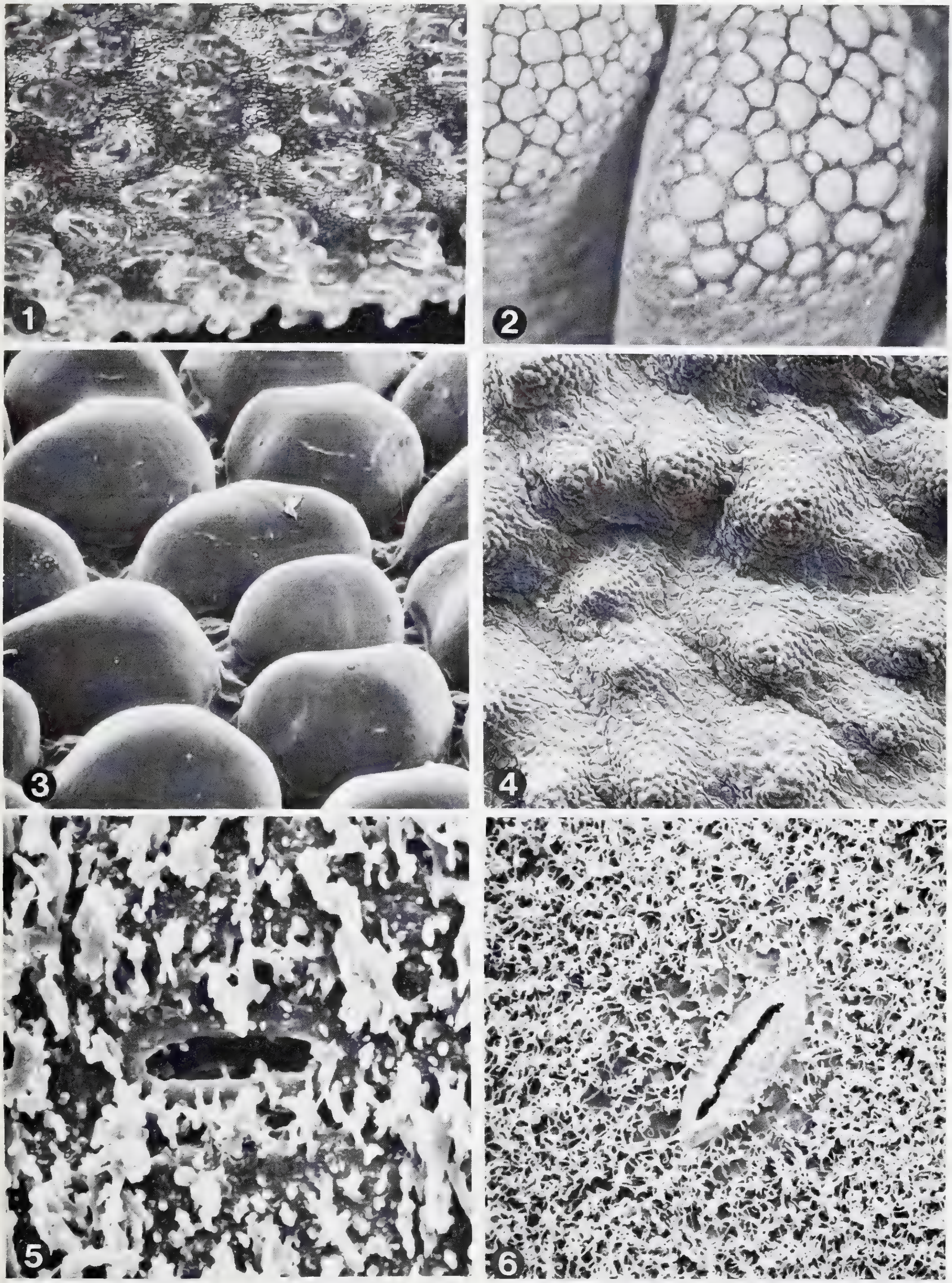

FIG. 3.—1, *Monilaria chrysoleuca* (Schltr.) Schwant. var. *chrysoleuca.* Idioblast type of epidermis. The huge idioblasts with papilla-like protuberances are 0,6 mm long and 0,5 mm high; they represent surface sculptures of size class I. Macrophotograph, × 2,5. 2, *Titanopsis schwantesii* (Dtr.) Schwant. Xeromorphic type of epidermis. The leaf tips exhibit elevations (diameter 0,5–1 mm) of the epidermis formed by groups of epidermal cells; these elevations represent surface sculptures of size class I. Macrophotograph, × 5. 3, *Jacobsenia kolbei* (L. Bol.) L. Bol. (*Ihlenfeldt & Poppendieck* 6376). Idioblast type of epidermis. The SEM photograph shows the protruding idioblasts, the much smaller 'ordinary' epidermal cells and the stomata. × 200. 4, *Stomatium* sp. cf. *S. bolusiae* Schwant. Xeromorphic type of epidermis. The SEM photograph shows elevated areas (forming sculptures of size class I, compare Fig. 3.2) and depressed areas; the stomata are confined to the depressed areas. × 50. 5, *Prenia vanrensburgii* L. Bol. Idioblast type of epidermis. The wax cover forms platelets representing sculptures of size class III. × 2000. 6, *Malephora* sp. (*Hartmann* 1460). Idioblast type of epidermis, but idioblasts much reduced (compare Fig. 5.6). The wax cover forms thread-like structures representing sculptures of size class III. × 2000.

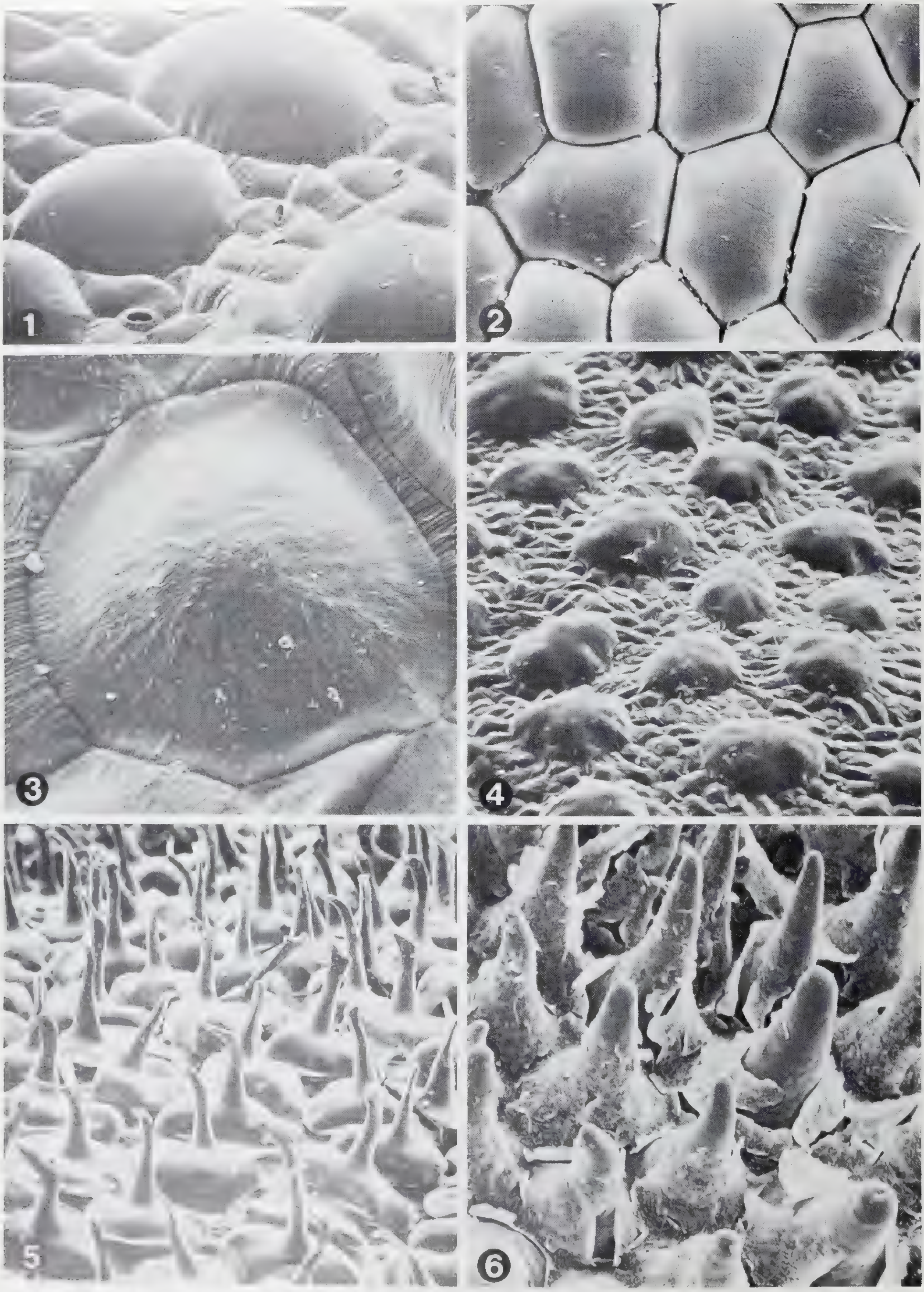

FIG. 4. 1, *Prenia relaxata* (Willd.) N.E. Br. Idioblast type of epidermis. The idioblasts are only slightly raised. 2, *Jacobsenia kolbei* (L. Bol.) L. Bol. (*Hartmann* 1641). Idioblast type of epidermis. The idioblasts are so densely crowded that the 'ordinary' epidermal cells and the stomata are not visible from above. Note that there is a considerable variation in the idioblast pattern within the species (compare Fig. 3.3). × 200. 3, *Prenia sladeniana* (L. Bol.) L. Bol. Idioblast type of epidermis. The idioblasts are only very slightly raised. × 500. 4, *Aptenia* sp. (*Ihlenfeldt & Poppendieck* 6362, undescribed species). Idioblast type of epidermis. The idioblasts exhibit dome-like protrusions. × 100. 5, *Jacobsenia hallii* L. Bol. Idioblast type of epidermis. The idioblasts exhibit papilla-like protuberances, which represent sculptures of size class II. Note that only the idioblasts are capable of forming papillae (compare Fig. 4.6). × 180. 6, *Cheiridopsis* sp. (*Ihlenfeldt, Jürgens & Bittrich* 9133). Isomorphic type of epidermis. All epidermal cells (except guard cells and subsidiary cells) form papilla-like protuberances, which represent sculptures of size class II. The wax cover is continuous (partly detached due to preparation). × 500.

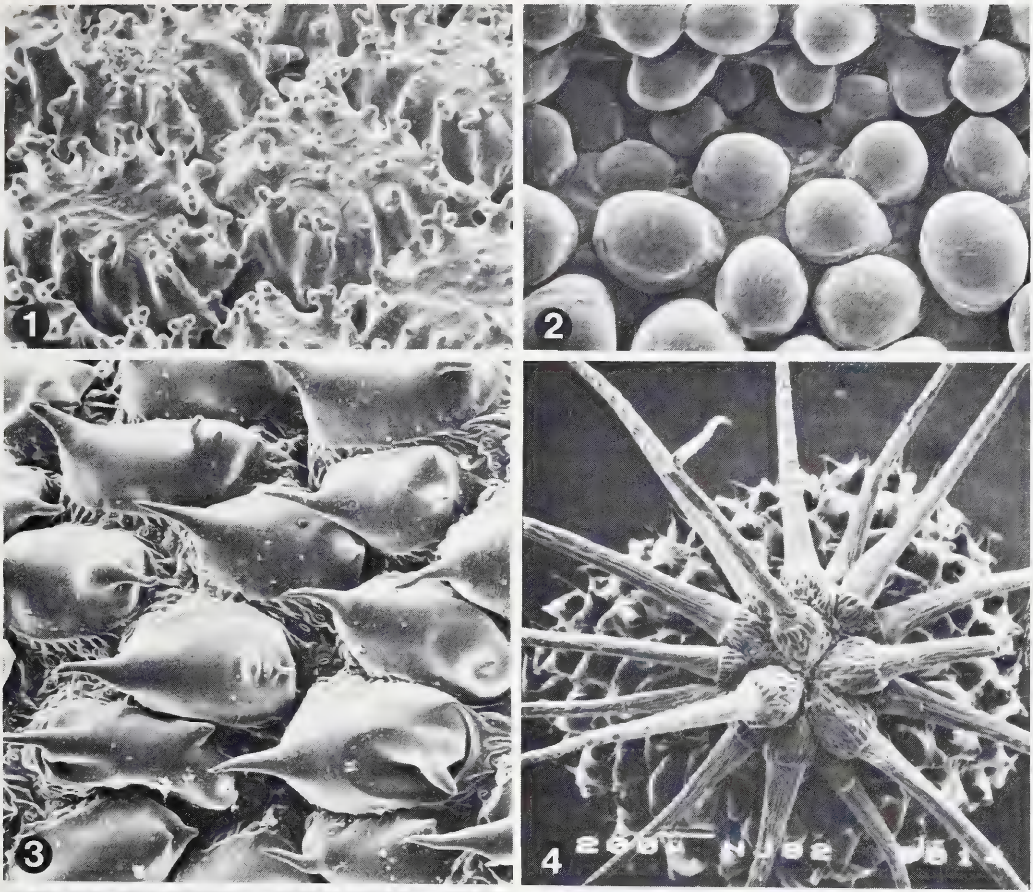

FIG. 5.—1, *Anisocalyx vaginatus* (L. Bol.) L. Bol. Idioblast type of epidermis. The idioblasts (sculptures of size class I) exhibit a series of branched antler-like protuberances representing sculptures of size class II. 2, *Prenia sladeniana* (L. Bol.) L. Bol. Idioblast type of epidermis. The margins of two leaves within the bud interlock by their idioblasts which along the margin are much more raised than on the rest of the leaf (compare Fig. 4.3). 3, *Trichodiadema* sp. cf. *T. bulbosum* (Haw.) Schwant. Idioblast type of epidermis. Each idioblast exhibits two (sometimes three) papilla-like protuberances (representing sculptures of size class II). The large one is directed towards the tip of the leaf. The adjacent 'ordinary' epidermal cells form a sort of cup around the base of each idioblast. 4, *Trichodiadema* sp. cf. *T. bulbosum*. Leaf tip with the characteristic 'hair bristle' (diadema). The long hairs originate ontogenetically from idioblasts (compare Fig. 5.3) and are able to absorb water (see Ihlenfeldt, 1980). × 45. 5, *Disphyma crassifolium* (L.) L. Bol. Idioblast type of epidermis, but the idioblasts are extremely reduced (one single idioblast can be seen near the centre of the picture). × 500. 6, *Malephora* sp. (*Hartmann* 1879). Idioblast type of epidermis. As in *Disphyma,* the idioblasts are extremely reduced except along the margin of the leaf at the tip. × 100.

'normal' condition in the native habitats), is invested in these structures. The ecological significance of the sculptures can furthermore be deduced from the fact that *analogous* structures occur in different groups of the family, all living in similar habitats.

As far as the xeromorphic type of epidermis is concerned, this concept is consistent with the 'classical' views on ecological significance of the so-called xeromorphic features of an epidermis. The idioblast type of epidermis, however, according to current views, must be called aberrant if one takes into account, that representatives of both types of epidermis can occur sympatrically in the same extreme habitat (e.g. *Oophytum* N.E.Br., idioblast type of epidermis, and *Argyroderma* N.E.Br., xeromorphic type. Ihlenfeldt & Hartmann 1982). Furthermore, the remarkable tendency towards an enormous enlargement of the surface of *living* epidermal cells by various types of protuberances is poorly understood, since xerophytes are thought to display a tendency towards reducing their surface in order to decrease water loss by cuticular transpiration.

At present we are far from a thorough understanding of the functioning of the two basic types of epidermis and of the ecological significance of certain features, especially of the sculptures. The following remarks are only tentative and more or less hypothetical; they are made to indicate possible directions of future research.

Ecophysiological investigations (Von Willert *et al.*, 1980) have revealed that the two different basic types of epidermis apparently are the anatomical expression of two different life strategies or survival strategies under very extreme conditions. The one group (species with an epidermis of the idioblast type) may be called the 'opportunists', the other group (species with an epidermis of the xeromorphic type) the 'savers'. The 'opportunists' have a comparatively high water turnover (relying on their ability of compensating losses during the night, see below) with the advantage of a higher output from photosynthesis (which makes possible a high growth rate) on the one hand and on the other hand with the risk of death under abnormal drought conditions, when the mechanism for extracting water from the atmosphere no longer works. The 'savers' minimize their water losses under all (even under favourable) conditions; under extreme conditions, such as prolonged periods of drought, they successfully rely on their water reserves, stored in the centre of their leaves, and on the high degree of protection against water loss by the xeromorphic type of epidermis. The first group can take advantage of periods with rainfall above average and survives in periods of prolonged drought only by seeds; the second group is more successful in surviving in the form of adult individuals in periods with rainfall below average. This could cause drastic oscillations in the composition of a given plant community formed by species with both types of epidermis (and both types of life strategies). Yet, considered over a long period, the frequencies of species with different life strategies and the total amount of biomass represented by the two groups, should remain unchanged, since statistically, favourable and unfavourable periods will follow each other.

How the method of gaining water, well developed in the group with an epidermis of the idioblast type, functions, is still being examined. There are indications, that the idioblasts are involved. The ability of the idioblasts to change their shape according to water supply of the plant, has already been mentioned; in this connection, one should remember that the apertures of the stomata are nearly always parallel to the outline of the adjacent idioblasts. It might be that by changing their shape the idioblasts directly induce the opening and closing of the stomata (Von Willert, pers. comm.), i.e. that the idioblasts act as regulators of the stomata proper ('super-stomata'). Furthermore, in this connection, it appears significant that the idioblasts contain numerous mitochondria and chloroplasts, which indicates high physiological activity, at least at certain times. Notwithstanding the fact that water stored in the idioblasts can be withdrawn to compensate for extreme losses of water elsewhere in the plant, the view that the idioblasts serve an external water storage function, first expressed by Volkens (1887) and again, slightly modified and stressed by Steudle *et al.* (1975), certainly is too simple.

The two basic types of epidermis also exhibit differences in their optical properties affecting radiation balance. In the range of wave lengths from 400–1 300 nm (i.e. all relevant wave lengths, see Eller, 1979) the idioblast type of epidermis has a low rate of reflection and a high rate of transmission. In contrast, the xeromorphic type of epidermis exhibits a high rate of reflection (probably caused by the oxalate crystals in the outer cell wall of the epidermis) and a relatively low rate of transmission (apparently due to the fact that the leaves are isolateral; light once having passed the epidermis, is reflected at the same high rate by the epidermis of the opposite side, i.e. it is 'trapped'). It should be stressed that the rate of absorption (and transmission) is in the first place determined by the diameter of tissue passed by the radiation. Therefore, the two examples given in Fig. 6 represent plants with comparable diameters of leaf; the rate of absorption is nearly equal in both species (unpublished data by Eller).

The role of the complicated sculptures is still poorly understood. Sculptures of size class III, formed by the wax cover, can influence the radiation balance as has been demonstrated in succulent plants of other families (Eller, 1979); the same may be true for the Mesembryanthemaceae. Sculptures of size class I and II may influence energy (heat) exchange between the leaf surface and the surrounding air. Barthlott & Wollenweber (1981) have advanced the hypothesis that sculptures of these dimensions enhance turbulence on the leaf surfaces, thus reducing the heat stress of the leaves during day time. However, these sculptures may have quite a different function during the night. The water uptake from the atmosphere during the night, well developed in species with the idioblast type of epidermis, is probably triggered or enhanced by a

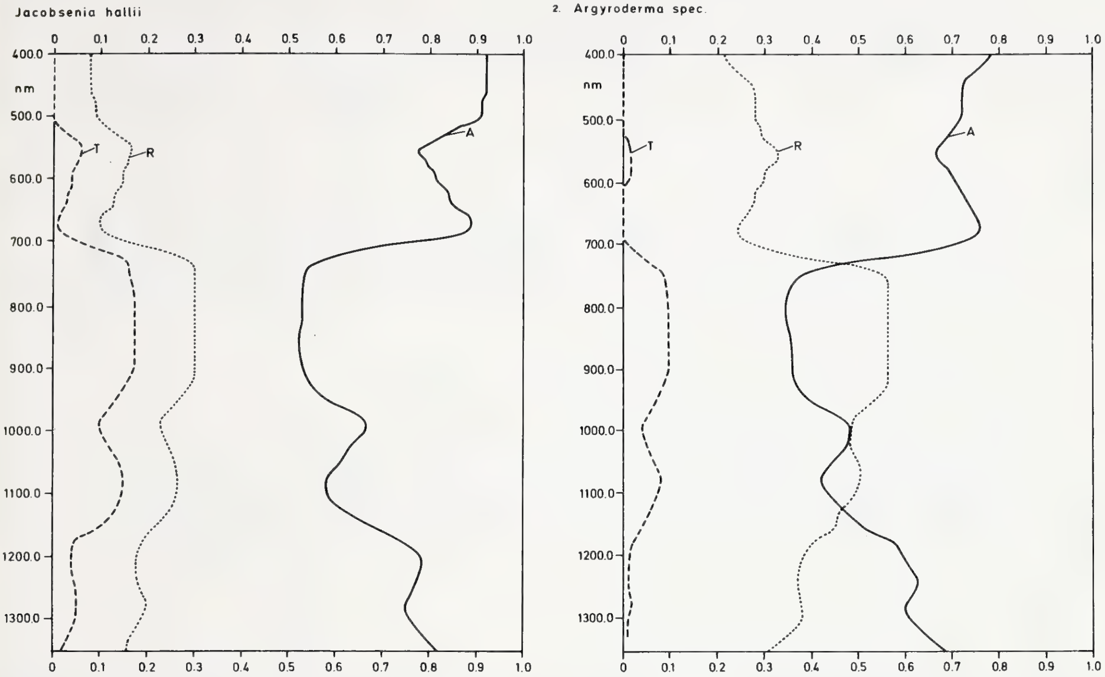

FIG. 6.—Optical properties of leaves exhibiting the two basic epidermis types. Ordinate: wave lengths in nm; abscissa: ratio. T= Transmission (i.e. light having passed the leaf); R = reflection; A = absorbtion. *Jacobsenia hallii* L. Bol. (1) possesses an epidermis of the idioblast type (compare Fig. 4.5), whereas *Argyroderma* (2) possesses an epidermis of the xeromorphic type. For details compare text. (By courtesy of Dr B. Eller, unpublished data; for technical details see Eller, 1979.)

cooling down of the leaf surface to below the temperature of the surrounding air. This, obviously, is an effect of radiation, since this phenomenon can only be observed if the sky is cloudless (space acting as an energy sink). The cooling down leads to a considerable increase of relative humidity next to the surface of the leaf. Calculations (see Von Willert *et al.*, 1980) revealed that under favourable conditions of temperature (below 15°C) and of relative air humidity (above 80%), a positive vapour gradient is established from outside the leaf to inside. These conditions occur often during night time in the native habitats, especially during the winter season. As soon as the gradient has been formed, plants with the idioblast type of epidermis very suddenly open their stomata (possibly directed by or through influence of the idioblasts, see above). As a consequence, malate formation starts and apparently the uptake of water, too. It may be suggested that the complicated sculptures of size class I and II influence temperature balance by suppressing or inhibiting microconvection on the leaf surface that should equalize differences in temperature between leaf surface and surrounding air. This presumption is supported by the observation that differences in temperature can only be measured as long as the weather is calm (Von Willert *et al.*, 1980), which, in contrast to day time, is the usual condition during the night in the native habitats.

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Ten interesting species of aquatic Hyphomycetes from South Africa

R. C. SINCLAIR* and A. EICKER*

ABSTRACT

Examination of the foam spora of South Africa has revealed the presence of ten interesting species from nine genera, seven of which are new records for the African continent and three for South Africa. These are *Anguillospora crassa* Ingold, *Condylospora spumigena* Nawawi, *Flabellospora verticillata* Alasoadura, *Lateriramulosa uni-inflata* Matsushima, *Lemonniera alabamensis* Sinclair & Morgan-Jones, *Lemonniera filiformis* Petersen ex Dyko, *Lunulospora cymbiformis* Miura, *Speiropsis irregularis* Petersen, *Tetrachaetum elegans* Ingold and *Tricellula aquatica* Webster.

RÉSUMÉ

ESPÈCES INTÉRESSANTES D'HYPHOMYCÈTES AQUATIQUES D'AFRIQUE DU SUD

L'examen des spores présentes dans l'écume des eaux en Afrique du Sud a révélé la présence de dix espèces intéressantes appartenant à neuf genres; sept d'entre elles sont relevées pour la première fois sur le continent africain et trois en Afrique du Sud. Ce sont: Anguillospora crassa *Ingold,* Condylospora spumigena *Nawawi,* Flabellospora verticillata *Alasoadura,* Lateriramulosa uni-inflata *Matsushima,* Lemonniera alabamensis *Sinclair & Morgan-Jones,* Lemonniera filiformis *Petersen ex Dyko,* Lunulospora cymbiformis *Miura,* Speiropsis irregularis *Petersen,* Tetrachaetum elegans *Ingold et* Tricellula aquatica *Webster.*

INTRODUCTION

The following are some preliminary results of an extensive project under way to document the aquatic hyphomycete flora in South Africa. Among the many well-known aquatic hyphomycetes recovered and the many resulting taxonomic problems generated are ten interesting fungi, each of which is at least a new record for the Republic. Subsequent publications by the authors will include complete lists of all the fungi recorded.

At various sites throughout South Africa, foam samples were recovered from flowing fresh waters and fixed with IKI immediately to prevent germination of the spores. Within no specific time period the samples were filtered through 8 μm pore size millipore filters. The specimens thus collected were mounted in lactophenol cotton blue and identifications made on spore morphology.

AQUATIC HYPHOMYCETES

Anguillospora crassa *Ingold* (Fig. 1A). England is the type locality of this fungus (Ingold, 1958b) and it appears to have a ubiquitous distribution being recorded from Hungary, (Gonczol, 1971), Sweden and Tanganyika (Nilsson, 1964), U.S.A. (Petersen, 1962), West Indies (Hudson and Ingold, 1960), East New Guinea (Tubaki, 1965), Japan (Miura, 1974; Tubaki, 1960) and India (Thakur, 1977). Ingold's (1958b) type is 120–200 μm long × 15–20 μm wide. Frequently our specimens as well as some of other authors (Tubaki, 1960) are up to 4–5 μm narrower. One specimen from the Politsi River in the Debengeni Forest Reserve in the N.E. Transvaal was 225 μm long. Another spore from the same locality was markedly attenuate as figured. *A. crassa* is a new record for South Africa.

Collections examined:

TRANSVAAL. — 2330 (Tzaneen): Politsi River tributary, Magoebaskloof, Debengeni Forest Reserve (–CC), 17 Aug. 1979, R. C. Sinclair. 2430 (Pilgrim's Rest): Blyde River at Junction Hoedspruit-Strijdom Tunnel (–BC), 18 Aug. 1979, R. C. Sinclair; near Mariepskop on Mariepskop-Klaserie Road (–DB), 18 Aug. 1979, R. C. Sinclair. 2530 (Lydenburg): near Sabie (–BB), 19 Aug. 1979, R. C. Sinclair.

CAPE. — 3319 (Worcester): Entrance to Bainskloof Pass, Wellington (–CA), 31 Oct. 1980, A. Eicker.

Condylospora spumigena *Nawawi* (Fig. 1B). Malaysia is the type locality of this fungus (Nawawi, 1976a), although it has often been recorded elsewhere prior to description. *Obstipispora chewaclensis* Sinclair & Morgan-Jones (Sinclair & Morgan-Jones, 1979a) described from Alabama, U.S.A. is very likely the same fungus. It has also been recorded from Japan (Miura, 1974; Tubaki, 1960, 1966), Papua, New Guinea (Tubaki, 1965) and India (Ingold & Webster, 1973). Nawawi's (1976a) type is 10–15 septate and has an overall length of 72–104 μm with a 30–120° bend about halfway through the length with the proximal half being longer. One spore collected near Mariepskop Air Force Base in the N.E. Transvaal was unusual in having no septa and an extra 180° sigmoid bend fitted tightly next to the normal flexion. This may represent a new species. Another spore, as figured, from the same locality has 2 more septae than the type. This spore also has a shorter proximal half which is slightly swollen being 1–2 μm wider than the type but is probably close enough to be considered the same species. Ingold (1956) illustrated a spore closely similar to *C. spumigena* from a river in Ibadan, Nigeria although positive diagnosis is not certain. These collections, therefore, are new records for the African continent.

Collections examined:

TRANSVAAL. — 2330 (Tzaneen): Politsi River tributary, Magoebaskloof, Debengeni Forest Reserve (–CC), 17 Aug.

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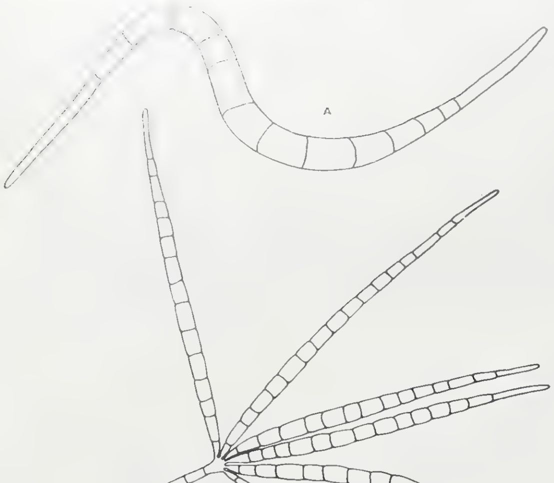

FIG. 1.—A, *Anguillospora crassa;* B, *Condylospora spumigena;* C, *Flabellospora verticillata;* D, *Lateriramulosa uni-inflata.*

1979, R. C. Sinclair. 2430 (Pilgrim's Rest): near Mariepskop Air Force Base (−DB), 18 Aug. 1979, R. C. Sinclair; near Mariepskop on Mariepskop-Klaserie Road (−DB), 18 Aug. 1979, R. C. Sinclair.

NATAL. — 2732 (Ubombo): Mbazwana Road, Sordwana Bay, Zululand (−BC), 31 Jan. 1981, J. V. van Greuning.

CAPE. — 3318 (Cape Town): Kirstenbosch Botanic Gardens (−CD), 21 June 1979, R. C. Sinclair; Table Mountain, near cable station (−CD), 21 June 1979, R. C. Sinclair; Eerste River, Jonkershoek near research facilities at Assegaaibosch (−DD), 21 June 1979, R. C. Sinclair. 3319 (Worcester): entrance to Bainskloof Pass, Wellington (−CA), 31 Oct. 1980, A. Eicker; Darling Bridge over Bainskloof River (−CA), 31 Oct. 1980, A. Eicker.

Flabellospora verticillata *Alasoadura* (Fig. 1C). Nigeria is the type locality of this fungus. Prior to description (Alasoadura, 1968) it was figured as unknown conidia from the U.S.A. (Conway, 1970), West Scotland (Ingold, 1973), West Indies (Hudson & Ingold, 1960), Papua, New Guinea (Tubaki, 1965) and on the African continent from Nigeria (Ingold, 1956, 1959), Sierra Leone (Le'John, 1965), Ghana (Dixon, 1959) and Uganda (Ingold, 1958a). Of all of these records, only that from the U.S.A. indicates the presence of the main axis 'stalk' cell generically characteristic for *Flabellospora.* Ingold's (1973) West Scotland collection does not agree geographically as Alasoadura (1968) concluded the fungus is tropical in nature. Since description, only a Malaysian collection (Nawawi, 1976b) has been positively identified. Our South African collection, from a border zone between temperate and subtropical climates, is a new record for the Republic.

Collection examined:

TRANSVAAL. — 2430 (Pilgrim's Rest): near Mariepskop on Mariepskop-Klaserie Road (−DB), 18 Aug. 1979, R. C. Sinclair.

Lateriramulosa uni-inflata *Matsushima* (Fig. 1D). New Britain of the Solomon Islands is the type locality of this fungus (Matsushima, 1971). Prior to description this fungus was figured from England (Ingold & Ellis, 1952) and the U.S.A. (Crane, 1968). It has, since description, been recorded from Japan (Miura, 1974) and Czechoslovakia (Marvanova, 1973). Although this species is most often recorded as foam spora, the type was described from leaves in a terrestrial habitat. Marvanova (1973) believes this hyphomycete to be 'water borne' rather than truly aquatic. One of our collections from the area near Mariepskop Air Force Base differs slightly from the type in that the singly opposing branch is not as inflated at the base. Our collections are a new record for the African continent.

Collections examined:

TRANSVAAL. — 2430 (Pilgrim's Rest): near Mariepskop Air Force Base (−DB), 18 Aug. 1979, R. C. Sinclair; near Mariepskop on Mariepskop-Klaserie Road (−DB), 18 Aug. 1979, R. C. Sinclair. 2431 (Acornhoek): junction of Klaserie and Mariepskop Road (−CA), 17 Aug. 1979, R. C. Sinclair.

Lemonniera alabamensis *Sinclair & Morgan-Jones* (Fig. 2A). Previous records of this fungus are known only from the type locality, Alabama, U.S.A. (Sinclair & Morgan-Jones, 1979b). Among our collections there appears to be more variability in the number of septa per radiating branch. The type specimen is described as having 2 septa per branch but our specimens vary in having from 1−4. One collection from the Stellenbosch area was significantly larger, the branches being 55−65 μm × 3,5 μm as opposed to 30−35 μm × 2−3 μm of the type. This specimen is intermediate between *L. alabamensis* and *L. centrosphaera* Marvanova (Descals, Webster & Dyko, 1977). These collections are new records for the African continent.

Collections examined:

TRANSVAAL. — 2430 (Pilgrim's Rest): near Mariepskop on Mariepskop-Klaserie Road (−DB), 18 Aug. 1979, R. C. Sinclair. 2431 (Acornhoek): junction of Klaserie and Mariepskop Road (−CA), 17 Aug. 1979, R. C. Sinclair.

ORANGE FREE STATE. — 2828 (Bethlehem): Golden Gate Highlands Park (−DA), 14 March 1979, R. C. Sinclair.

CAPE. — 3318 (Cape Town): Eerste River on Stellenbosch University grounds (−DD), 21 June 1979, R. C. Sinclair.

Lemonniera filiformis *Petersen ex Dyko* (Fig. 2B). New York, U.S.A. is the type locality of this species and it has only been recorded elsewhere in England (Descals, Webster & Dyko, 1977). Our collections are therefore new records for the African continent.

Collections examined:

TRANSVAAL. — 2330 (Tzaneen): Politsi River tributary, Magoebaskloof, Debengeni Forest Reserve (−CC), 17 Aug. 1979, R. C. Sinclair. 2430 (Pilgrim's Rest): Blyde River at

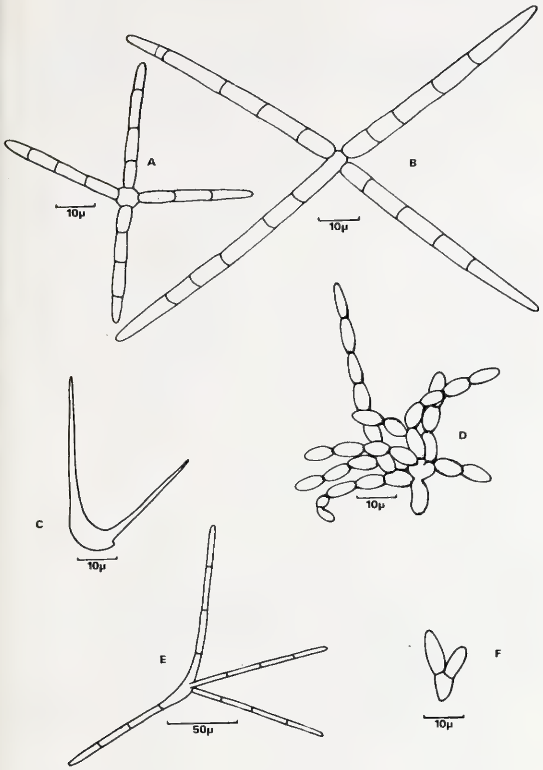

FIG. 2.—A, *Lemonniera alabamensis;* B, *Lemonniera filiformis;* C, *Lunulospora cymbiformis;* D, *Speiropsis irregularis;* E, *Tetrachaetum elegans;* F, *Tricellula aquatica.*

junction of Hoedspruit-Strijdom Tunnel (−BC), 18 Aug. 1979, R. C. Sinclair; near Mariepskop on Mariepskop-Klaserie Road (−DB), 18 Aug. 1979, R. C. Sinclair. 2431 (Acornhoek): junction of Klaserie and Mariepskop Road (−CA), 17 Aug. 1979, R. C. Sinclair.

Lunulospora cymbiformis *Miura* (Fig. 2C). The type locality is Japan and has only been recorded from other localities in that country (Miura, 1972, 1974). Our records are therefore new to the African continent.

Collections examined:

TRANSVAAL. — 2330 (Tzaneen): Politsi River tributary, Magoebaskloof, Debengeni Forest Reserve (−CC), 17 Aug. 1979, R. C. Sinclair. 2530 (Lydenburg): near Sabie (−BB), 19 Aug. 1979, R. C. Sinclair.

ORANGE FREE STATE. — 2828 (Bethlehem): Golden Gate Highlands Park (−DA), 14 March 1979, R. C. Sinclair.

CAPE. — 3318 (Cape Town): Eerste River, on Stellenbosch University grounds (−DD), 30 Oct. 1979, A. Eicker.

Speiropsis irregularis *Petersen* (Fig. 2D). New York, U.S.A. is the type locality of this species (Petersen, 1963). Prior to description, spores of this fungus appear to have been recorded among unknown conidia types from Canada (Ingold, 1960a) and Hungary (Gonczol, 1971). Subsequent to description, Miura (1974) recorded this fungus from Japan but we question his identification. From his illustration one does not get the impression that the spore developed as a result of acropetal cell proliferation as is described for the type of the genus, *Speiropsis pedatospora* Tubaki (Tubaki, 1958), as well as for the type of Petersen's species. Our collections are new records for the African continent.

Collections examined:

TRANSVAAL. — 2430 (Pilgrim's Rest): near Mariepskop Air Force Base (−DB), 18 Aug, 1979, R. C. Sinclair; near Mariepskop on Mariepskop-Klaserie Road (−DB), 18 Aug. 1979, R. C. Sinclair.

Tetrachaetum elegans *Ingold.* (Fig. 2E). The type locality is England (Ingold, 1942). This species is cosmopolitan having been recorded from such widespread areas as Ireland (Fenton, 1950), Sweden (Nilsson, 1958), Hungary (Gonczol, 1971), Australia (Cowling & Waid, 1963), Japan (Tubaki, 1960; Miura, 1974) Hawaii (Ranzoni, 1979), and the U.S.A. (Peterson, 1963). Ingold (1958, 1960b) has made collections of this species from Zimbabwe. Our collections are therefore new to South Africa.

Collections examined:

TRANSVAAL. — 2330 (Tzaneen): Politsi River tributary, Magoebaskloof, Debengeni Forest Reserve (−CC), 17 Aug. 1979, R. C. Sinclair. 2530 (Lydenburg): near Sabie (−BB), 19 Aug. 1979, R. C. Sinclair.

Tricellula aquatica *Webster* (Fig. 2F). For this species there is only the type locality, England (Webster, 1959) and one other England collection (Hudson & Sutton, 1964) on record. Our collections from the Olifants River, Transvaal show a wide range of spore sizes, up to twice the size of the type, as figured herein. Some of these larger spores may bear septa in the apical cells. It is possible that they are either unusual forms of the fungus or represent a new species. Further work will clarify this. These collections are new records for the African continent.

Collections examined:

TRANSVAAL. — 2330 (Tzaneen): Politsi River tributary, Magoebaskloof, Debengeni Forest Reserve (−CC), 17 Aug. 1979, R. C. Sinclair. 2430 (Pilgrim's Rest): Olifants River, Manoutsa Park (−BC), 18 Aug. 1979, R. C. Sinclair.

ACKNOWLEDGEMENTS

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Register of names and types in Poaceae: a computerized index for southern Africa

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ABSTRACT

For each name based on or applied to southern African grasses the following data is recorded: name, author, place and date of publication, basionym, cross-reference to other genera, and type specimens. The data is entered into a computer file for sorting in the following ways: by name alphabetically, by place of publication, by genus or by collector of the type specimen. The lists thus produced are directly useful for taxonomic study, and will also be the basis for efforts by staff of the Botanical Research Institute, Pretoria, to acquire copies of all original descriptions and photographs of all type specimens. The methods for compiling the Register worked out for Poaceae can be applied to registers of names in other plant families.

RÉSUMÉ

LISTE DES NOMS ET DES TYPES DE POACÉES: UN INDEX INFORMATISÉ POUR L'AFRIQUE AUSTRALE

Pour chaque nom de graminée d'Afrique australe qu'il soit basé ou non sur du matériel de cette region les données suivantes sont enregistrées: nom, auteur, référence bibliographique, basionyme, synonymie et spécimens types. Les données sont entrées dans un fichier d'ordinateur pour le triage de la façon suivante: par ordre alphabétique des noms par référence bibliographique, par genre ou par récolteur du spécimen type. Les listes ainsi produites sont directement utiles pour l'étude taxonomique et elles serviront aussi de base au personnel de l'Institut de Recherche Botanique de Pretoria pour tenter d'obtenir les descriptions originales et les photographies de tous les spécimens types. Les méthodes de compilation élaborées pour les Poacées peuvent être appliquées à d'autres familles.

INTRODUCTION

Why a Register?

The most tedious part of taxonomic work is listing the names that must be evaluated in a taxon, finding the original descriptions and borrowing the type specimens for examination. If copies of original descriptions and photographs of type specimens for all names based on or applied to southern African taxa were present in the Botanical Research Institute, the progress of the Flora of Southern Africa would be more rapid because the waiting time for obtaining these from overseas would be eliminated.

Why computerize?

The register of names has been computerized rather than maintained on a card file, because it can be sorted in various ways and printed by machine, depending on the purpose for which the data is required. The major disadvantage of the computer is the practical difficulty of exact data input, but it is outweighed by the ease with which the same data can be correctly printed again and again in various combinations once it has been correctly entered. Thus the proofreading and correcting of the data file, although seemingly an unending task at the time the data is entered, are not repeated afterwards no matter how many times and in what combinations the data is sorted and printed.

METHOD

Names were found by searching *Flora Capensis, Index Kewensis,* Chase & Niles (1962) *Index to Grass Species, AETFAT Index, Kew Record,* and older floristic and monographic studies. For each name the following data was recorded on encoding forms and entered in a data file on the Department of Agriculture and Fisheries Burroughs 7100 computer:

Name and author

Place and date of publication

Basionym

Cross-reference to other genera

Type specimens

Each entry occupies six lines in the data file, with two lines provided for type specimens, as shown in Fig. 1. If there are more than two syntypes for a name, the first four lines are repeated with the additional types.

Programs have been written to sort the entries in four ways, each of which has a different application.

1. Sorted by name alphabetically. In its entirety, this provides an alphabetical list of all southern African grass names, which is used to locate names missing from the Register by checking additional references against the existing Register.

2. Sorted by reference alphabetically and by page number. This list will be the basis for locating and obtaining original descriptions for all names. With the names listed by the references in which they were first described, it will be a straightforward matter to extract all descriptions needed from each reference. Once the original descriptions are

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AFRACHNERIA ECKLONII (NEES) ADAMSON
    JL. S. AFR. BOT. 005:0053 (1939)
    ERIACHNE ECKLONII NEES, FL. AFR. AUSTR. 0273  (1841)
    PENTASCHISTIS
    ECKLON CAPE - TULBAGH
    DREGE 1660 KLEIN DRAKENSTEIN AD FLUMEN BERGRIVIER ALT 400'
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FIG. 1.—A complete entry in the Register. Line 1 = name and author; Line 2 = place of publication; Line 3 = basionym; Line 4 = cross-reference to other genera; Lines 5 & 6 = type specimens.

available, it will then be possible to determine the type specimen for each name, and to add this information to each entry in the Register, if it was not known at the time the entry was first made.

3. Sorted by genus. All the names that are applicable to a particular genus are listed alphabetically, whether the genus appears as part of the name, in the basionym, or as a cross-reference to other genera. This is most useful to monographers because it gives direct access to all the names that apply to any genus.

4. Sorted by collector. Once all type specimens are entered in the Register, it will be useful to list the specimens of each collector that are known to be types. These specimens can be sought in different herbaria, and photographed for the use of taxonomists at the Botanical Research Institute.

RESULTS AND DISCUSSION

About 4 200 names have been recorded for the Poaceae, which has about 850 indigenous species in southern Africa. Most of these names have been found, encoded and entered in the computer by technical assistants, thus saving the time of professional staff. Furthermore, by finding the names for the entire family at one time, much of the repetition of looking through the same reference volumes for each of the 210 genera separately has been avoided.

The copying of all original descriptions and locating and the photographing the type specimens still lie in the future. However, the Register has already proved its worth to the progress of the Flora of Southern Africa in studies of the tribes Meliceae and Ehrharteae. It was possible to find all the names pertinent to the genera in these tribes immediately through the Register, and because of the cross-referencing system, it has been possible to examine relevant names which may not have been found in an [illegible] straightforward literature search for each genus. When working in a genus, the printout of names can be cut up and each name pasted to a file card. [illegible] and accuracy the index [illegible] by Leenhouts (1968) as a [illegible].

Because the Register of names for Poaceae is a forerunner for [illegible], it is worthwhile [illegible] in its development. The first of these is that the Register was begun a number of years ago as a file card system, contributed to by various individuals. It was therefore not possible to determine what original sources had been searched, and a great deal of the early work had to be repeated in order to ensure completeness. The second problem was that all the original cards had to be re-encoded in a format suitable for transfer to the computer. These two problems hopefully will not trouble future extensions of the Register to other families, because the format will be planned from the beginning. The third problem, the necessity for continuity of staff to do the encoding, entering and checking of data, is more serious. The required accuracy cannot be maintained when there is rapid turnover of inexperienced personnel.

ACKNOWLEDGEMENTS

Drs B. de Winter and P. J. Vorster have been associated with the Register from its beginning as a card index. Dr H. F. Glen wrote the computer programs for sorting the entries. Numerous individuals at the Botanical Research Institute have assisted in encoding and entering the data, especially Mrs C. Fourie and Mrs N van der Westhuizen.

CAVEAT

The author begs to inform reviewers and readers that this paper is written in her native language. Therefore the word *data* appears as a collective noun that is singular in number. A change to plural is expected*, and will be (barely) tolerated. However, it seems incredibly awkward.

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*In deference to the author's particularly strong feelings about *data* being a singular collective noun, the Editor has not made the necessary corrections.

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Weed flora of South Africa 1: major groupings

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ABSTRACT

Whilst attention has been focussed on combating priority weeds we have neglected to obtain an overall picture of our weed flora. To rectify the position a National Weed List has been compiled, the weeds have been classified and an analysis made of the weed flora. Aspects covered in this paper are: major taxa, exotic and indigenous species and kinds of weeds.

The presence of imbalances or power shifts between indigenous taxa is indicated by the fact that most weeds are supplied by a few families, and that Monocotyledon species are twice as likely to be weeds as are Dicotyledon species. The preponderance of Monocotyledon weeds is explained by re-invasion of cultivated and abandoned fields in grassland areas rather than by a shift towards Monocotyledon species in the veld.

Exotic weeds contribute to imbalances via their greater versatility as well as by re-inforcing some taxa or kind of weed groupings at the expense of others. There is a power shift towards exotic Gymnosperms. Apart from flora weeds, exotics provide most agrestals, lawn weeds and weeds of planted pastures, and nearly as many ruderals as the indigenous species.

RÉSUMÉ

LA FLORE DES PLANTES NUISIBLES D'AFRIQUE DU SUD 1: PRINCIPAUX GROUPEMENTS

Tandis que l'attention se concentrait sur la lutte contre les plantes nuisibles prioritaires, on avait négligé la recherche d'une connaissance exhaustive de notre flore de plantes nuisibles.

Pour remédier à cette situation, on a établi un Catalogue national des plantes nuisibles, ces dernières ont été classées et leur flore a a fait l'objet d'un examen approfondi. Les aspects traités dans cette note sont: les principaux taxons, les espèces exotiques et indigènes et les diverses catégories de plantes nuisibles.

La présence de déséquilibres ou de changements de dynamisme entre taxons indigènes tient au fait que la plupart des plantes nuisibles appartiennent à quelques familles seulement et que les espèces monoctylédones ont deux fois plus de probabilité d'être des plantes nuisibles que les espèces dicotylédones. La prépondérance de plantes nuisibles monocotylédones résulte de la réinvasion des champs cultivés et abandonnés dans des régions herbeuses plutôt que par un changement favorable aux monocotylédones dans le veld.

Les plantes nuisibles exotiques contribuent à des déséquilibres par leur versatilité plus grande, de même qu'en renforcant certains taxa ou certaines catégories de groupements de plantes nuisibles aux dépens des autres. Il y a un changement de dynamisme en faveur des Gymnospermes exotiques. En dehors des plantes nuisibles de la flore, les exotiques fournissent la plupart des plantes agrestes, des mauvaises herbes des pelouses et des plantes nuisibles des pâturages artificiels, et à peu près autant de plantes rudérales que les espèces indigènes.

1. INTRODUCTION

In the past 20 years there has been a growing realization of the importance of weeds, not only as competitors with our crops and pastures, but also as invaders of natural vegetation and water-systems. Attention has rightly been focussed on pest plants such as *Stipa trichotoma* (nassella tussock), *Opuntia aurantiaca* (jointed cactus), the Australian *Hakea* and *Acacia* species, and *Eichhornia crassipes* (water hyacinth). Whilst these pest plants demand our attention and their control still stretches our resources to the limits, it is understandable that less obviously important weeds receive little attention.

The dangers are that: without assessment of weed status, *ad hoc* decisions may be made, and these can be costly; without monitoring of changes in weed status all chance of early control can be lost; without a picture of the weed scene as a whole *groups* of plants (whose component species may be relatively unimportant) can invade unnoticed and unchecked, and; without a knowledge of *all* the weeds of a particular crop or vegetation type, control of the most important species may achieve nothing more than opening the way to other species in the 'pecking order'.

The first step in obtaining a perspective of our weed flora, has been to draw up a National Weed List which, we hope, will provide a platform for decision-making in the fields of weed research, control and legislation.

2. THE NATIONAL WEED LIST

The National Weed List has been compiled from the literature, from herbarium records and by consulting correspondents (Balsinhas *et al.*, in press).

It has not been possible at this stage to check in any depth the weedy credentials of every species put forward for inclusion in the list. We have been guided by our correspondents working in weed-related fields such as pasture science, crop production and nature conservation. On their advice, we have taken a conservative line in not including all the less troublesome species associated with woody encroachment in the veld. Perhaps the best measure of the conservatism of our approach is that of the more than 20 000 vascular plant species indigenous to South Africa only 4–5% are presently

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included in the weed list. This compares with over 50% of the flora of the United States of America 'considered undesirable by some segment of society' (USDA Agricultural Research Services, 1970).

Initially the weeds in the list were classified according to taxa, and whether they were exotic or indigenous. A preliminary analysis at this stage (Wells *et al.*, 1981) showed, *inter alia*, that: the list contains the names of some 1 600 species; it is growing fast, with an ever-increasing proportion of indigenous species being regarded as weeds and; although our weeds (both indigenous and exotic) come from 137 plant families, over 50% of the species are supplied by six families (Poaceae, Asteraceae, Fabaceae, Cyperaceae, Solanaceae and Lamiaceae).

3. ANALYSIS OF OUR WEED FLORA

3.1 *Major taxa*

Since the first analysis was made, a few species of doubtful weediness have been eliminated from the list. It now contains the names of 1 573 species of which 56% are indigenous and 44% exotic.

The contributions of the major taxa, the Dicotyledons, Monocotyledons, Gymnosperms and Pteridophytes, to the list has been analysed in Tables 1, 2 and 3.

Nearly two-thirds of our indigenous weed species are Dicotyledons (almost all the rest are Monocotyledons). Indigenous Gymnosperms are particularly unaggressive and, though the ferns contain a number of weeds, very few are serious pests.

If the contribution of the major taxa is analysed in terms of species available that could have become weeds, then the Monocotyledons are seen to have by far the highest percentage of weediness—almost double that of the Dicotyledons.

Exotic weeds add only 3 to 4% in numbers of species to the three largest taxa (the Dicotyledons, Monocotyledons and Pteridophytes) but add over 24% to the Gymnosperms, indicating a possible shift in their favour.

In the Dicotyledons the numbers of indigenous and exotic weed species are almost equal, but in the Monocotyledons indigenous weed species outnumber exotics two to one. Whether this indicates that we have particularly aggressive indigenous Monocotyledons, ready to fill the available niches caused by disturbance, is not clear. It would be revealing to compare the South African figures with those of other countries to see whether this is a local or general phenomenon.

The Monocotyledons contain the highest percentage of indigenous, weedy genera and families — indicating that their richness in weedy species is not due to one species-rich family, the Poaceae, alone. Further investigation of this point reveals that although the Poaceae contributes nearly all (120 out of 145) of the *exotic* Monocot. weeds, it contributes only about half (155 out of 294) of the *indigenous* Monocotyledon weed species. Other Monocot. families that are major contributors of indigenous weed species are the Cyperaceae and the Liliaceae.

The exotic weed species (694 of them) belong to 384 genera, of which 218 (57%) are new to the country. Of the 90 families that they belong to, 10 are also new to the country.

3.2 *Kinds of weeds*

To evaluate these apparent changes in the fortunes of taxa, calls for further classification of our weed flora into different kinds of weeds (Table 4)

ruderals — weeds of waste places e.g. roadsides and old lands,
agrestals — weeds of crops, orchards and gardens,
silvicultural — weeds of forestry plantations,
floral — naturalized exotics that compete with the indigenous flora,
pastoral — weeds of grassland.

The percentages shown in Table 4 refer to the number of indigenous or exotic weeds in a particular category relative to the number of weeds classified (1 573). The percentages total well over 100, because many species occur as weeds in more than one catecory. For example, *Bidens pilosa,* the blackjack is both a ruderal and an agrestal and, since it is an exotic naturalized in the veld, it is also a flora weed.

To enable a clearer distinction to be drawn between weeds of the veld and other weeds it was

TABLE 1.—Indigenous and exotic weed species within major taxa in South Africa

Major taxa	(A) Total no. indigenous species	(B) Indigenous weed species	(C) % weediness $\frac{B}{A} \times 100$	(D) Exotic weed species	(E) Total weed species B + D
Dicotyledons	15 472	574	3,7	531	1 105
Monocotyledons	4 307	294	6,8	145	439
Gymnosperms	[illegible]	0	0	9	9
Pteridophytes	228	11	4,8	9	20
Total (vascular plants)	[illegible]	879	4,4	694	1 573

TABLE 2.—The numbers of indigenous and exotic weed genera within major taxa in South Africa

Major taxa	(A) Total no. indigenous genera	(B) Indigenous genera containing indigenous weed species	(C) % indigenous genera containing indigenous weeds $\frac{B}{A} \times 100$	(D) Genera containing exotic weed species		
				Indigenous genera	Exotic genera	Total
Dicotyledons	1 472	269	18	113	179	292
Monocotyledons	456	113	25	48	33	81
Gymnosperms	5	0	0	0	2	2
Pteridophytes	70	12	17	5	4	9
Total (vascular plants	2 003	394	20	166	218	384

TABLE 3. —The numbers of indigenous and exotic weed families within major taxa in South Africa

Major taxa	(A) Total no. indigenous families	(B) Indigenous families containing indigenous weed species	(C) % indigenous families containing indigenous weeds $\frac{B}{A} \times 100$	Families containing exotic weed species		
				Indigenous families	Exotic families	Total
Dicotyledons	159	73	46	63	6	69
Monocotyledons	36	19	53	12	2	14
Gymnosperms	5	0	0	0	1	1
Pteridophytes	27	8	30	5	1	6
Total (vascular plants)	227	100	44	80	10	90

necessary to subdivide the pastoral weeds category (Table 5).

The various kinds of weeds can be grouped according to the kind and degree of disturbance in their habitats, which is linked to their position in the plant succession.

The largest group are weeds of the veld, where disturbance results mainly from combinations of grazing and burning and where the communities may be pre- or post-climax. This group includes weeds of natural pastures, flora weeds and recreational weeds, totalling 1 088 species.

The next largest group are weeds of waste areas i.e. previously cleared areas at various stages of succession back to veld. These are the ruderals, totalling 835 species.

The last and smallest group are the weeds of areas that are maintained in a state of disturbance i.e. agrestal weeds, silvicultural weeds, lawn weeds and weeds of planted pastures, totalling 558 species.

3.2.1 *Kinds of weeds in major taxa*

Investigation of the weeds of major taxa that appear to be on the increase shows that:

(a) Most indigenous Monocotyledon weeds (including grasses) are agrestals and ruderals i.e. their preponderance does not reflect a power shift in the veld so much as attempts to re-invade cultivated and abandoned lands in areas naturally occupied by grassland.

(b) The exotic Gymnosperm weeds, on the other hand, are all weeds of the veld and their preponderance does reflect a power shift between major taxa.

3.2.2 *The contribution of exotics*

Exotic weeds are in the minority: 694 exotic species to 879 indigenous species (see Table 1) yet they figure in more ‘kind of weed’ categories — 1 275 to 1 206 (see Table 4). The species/category ratio is 1,8 for exotics and 1,4 for indigenous species, indicating that the exotics have, on the whole, considerably greater versatility as weeds than have the South African species in their home environment.

Indigenous species supply most pasture weeds, ruderals, silvicultural weeds and recreational weeds. Exotics provide all the flora weeds, most agrestals, lawn weeds and weeds of planted pastures, and

TABLE 4. —The distribution of indigenous and exotic weeds in 'kind of weed' categories

Kind of weed	Weed species					
	Indigenous		Exotic		Total	
categories	Number	% *	Number	% *	Number	% *
Ruderal	445	28	390	25	835	53
Agrestal	176	11	265	17	441	28
Silvicultural	48	3	24	2	72	5
Floral	0	0	481	31	481	31
Recreational	37	2	24	2	61	4
Pastoral	500	32	91	6	591	38
Total species in categories	1 206	76	1 275	83	2 481	159

* of 1 573 = total number of species in the Weed List.

TABLE 5.—The distribution of indigenous and exotic weeds in pastoral weed sub-categories

Kind of weed	Weed species		
Categories	Indigenous	Exotic	Total
Lawn	11	22	33
Planted pasture	4	8	12
Natural pasture	485	61	546
Total pastoral weeds	500	91	591

nearly as many ruderals as do the indigenous species.

3.3 *Further classification*

The sub-division of the pastoral weed category reveals how few weeds of planted pastures have been recorded. This is almost certainly a shortcoming of data gathering, and it is important since these weeds are likely to increase rapidly as efforts as veld improvement are stepped up.

It is our intention to continue sub-dividing and refining the 'kind of weed' categories and it is anticipated that they will become increasingly useful in weed control situations, as this is done. For example, weeds of natural pastures need to be further sub-divided according to veld types or similar vegetation units, and agrestal weeds need to be classified according to the crops where they cause problems.

The weeds in the national list have already been classified in terms of: region or origin, habitat favoured, weedy characteristics, useful characteristics, life cycle, reproduction, growth form and woodiness. These characteristics will be used in [illegible] of our weed flora and its effects.

[illegible]

[illegible] few families and [illegible] almost twice as likely to be [illegible] there appear to be imbalances or power shifts developing between indigenous taxa. Investigation shows that the preponderance of Monocotyledon weeds reflects reinvasion of cultivated and abandoned lands in grassland areas rather than a power shift towards Monocotyledons in the veld. The position at family and species level has still to be investigated.

Exotic weeds contribute to imbalances through their greater versatility as well as by reinforcing some taxa or kind of weed groupings at the expense of others. There is a power shift towards exotic Gymnosperms. Apart from flora weeds exotics provide most agrestals, lawn weeds and weeds of planted pastures, and nearly as many ruderals as do the exotic species.

Classification of weeds helps expand knowledge of our weed flora and helps identify areas where knowledge is lacking. It is essential that the process of classification and assessment should be continued to provide a broad base for weed research, control and legislation.

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Alien trees, shrubs and creepers invading indigenous vegetation in the Hluhluwe-Umfolozi Game Reserve Complex in Natal

I. A. W. MACDONALD*

ABSTRACT

The results of a survey and monitoring programme conducted in the Hluhluwe-Umfolozi Game Reserve Complex in Natal are presented. The area consists of 900 km^2 of savanna and forest vegetation.

Twenty alien tree, shrub and creeper species currently invading indigenous vegetation within the Complex are listed. Herbaceous aliens were not surveyed.

An analysis of the habitats being invaded by these alien plants is presented and it is concluded that riverine and forest-edge habitats are those most seriously threatened by alien plant infestations.

The distribution, nature and history of the infestations of each species are summarized. Distribution maps given for the eight species which are currently most important in the Complex. The potential threat posed by each species is estimated and the species are ranked in order of priority for control action.

The South American composite, *Chromolaena (Eupatorium) odorata,* is identified as being the alien species currently posing the greatest threat to natural vegetation in the Complex. The Asian tree, *Melia azedarach,* is considered the second most important alien species invading the area. It is concluded that both these species should be declared noxious weeds throughout the Republic and that research into their biological control is urgently required.

RÉSUMÉ

ARBRES, ARBUSTES ET PLANTES GRIMPANTES ÉTRANGÈRES ENVAHISSANT LA VÉGÉTATION INDIGÈNE DE LA RÉSERVE ANIMALE DU COMPLEXE DE HLUHLUWE-UMFOLOZI AU NATAL

Les résultats d'un inventaire et d'un programme d'observations suivies conduits dans la réserve animale du complexe Hluhluwe-Umfolozi au Natal sont présentés. La région consiste en 900 km^2 de savanne et de végétation forestière.

Vingt espèces d'arbres, d'arbustes et de plantes grimpantes étrangères qui envhaissent couramment la végétation indigène de ce complexe sont inventoriées. Les espèces herbacées étrangères n'ont pas été relevées.

Une analyse des habitats envahis par ces plantes étrangères est présentée et il en est conclu que les habitats riverains et de bordure de forêts sont ceux qui sont le plus sérieusement menacés par des infestations de plantes étrangères. La distribution, la nature et l'histoire des infestations de chaque espèce sont résumées. Des cartes de distribution sont données pour les huit espèces qui sont actuellement les plus importantes dans le complexe. La menace potentielle posée par chaque espèce est estimée et les espèces sont classées par ordre de priorité de lutte.

La composée sud-americaine, Chromolaena (Eupatorium) odorata, *est reconnue comme l'espèce étrangère posant la plus grande menace pour la végétation naturelle du complexe. L'arbre asiatique,* Melia azedarach, *est considéré comme la seconde espece en importance envahissant la région. En conclusion, ces deux espèces devraient être déclarées plantes nuisibles à travers toute la République et des recherches sur une lutte biologique contre elles est requise de toute urgence.*

INTRODUCTION

Alien plant species are widespread throughout Natal and a number of species have become naturalized and are competing successfully with the indigenous flora.

The overall impact that these aliens are having on the indigenous flora and fauna has never been assessed. However, as all plants compete for limiting resources (e.g. space, water, light, nutrients, pollination and dispersal vectors), it is safe to assume that any increase in an alien plant species can only occur at the expense of the indigenous flora. Any radical alteration of the flora is likely to be reflected in the fauna.

The overall management objective of the Hluhluwe-Umfolozi Game Reserve Complex (from now on called the Complex) is the long term maintenance of viable populations of as many of the indigenous species in the reserve as possible. This objective can only be achieved if the invasion of the area by alien plants is controlled. This study was carried out as part of the ongoing management of alien plant infestations in the Complex.

This paper condenses and updates information presented in an earlier more detailed report on the subject (Macdonald, 1978).

THE STUDY AREA

The Complex (see Fig. 1) is situated between latitudes 28°00' and 28°26' S and longitudes 31°43' and 32°09' E.

The environment and vegetation of the Complex are described by Whateley & Porter (1983). Plant species diversity is high with over 1 250 vascular plant species having been recorded of which 367 are woody trees and shrubs.

Faunal diversity is also high with the following number of species having been recorded from the

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* Hluhluwe Game Reserve, P. O. Box 25, Mtubatuba 3935, South Africa.

area: Amphibia, 26 (Bourquin *et al.*, 1971; P. J. Birkenstock, pers. comm.); Reptilia, 60 (Bourquin *et al.*, 1971); Aves, 400 (Macdonald & Birkenstock, 1980); Mammalia, 84 (Bourquin *et al.*, 1971).

During and for some years prior to this study the Complex as a whole was subjected to heavy grazing and browsing pressures from indigenous ungulate populations that have increased in density since the area was proclaimed a protected area in 1895.

An important management practice in the Complex is the controlled use of fire to manipulate plant communities. In general fire is confined to the grassland and open woodland communities in the Complex with closed woodland and forests tending to exclude fire. Burning is generally carried out at the end of the dry season (July to September) and on average some 23% of the surface area of the Complex is burnt each year (Macdonald *et al.*, 1980).

METHODS

Information on alien plants in the Complex was obtained in the following ways:

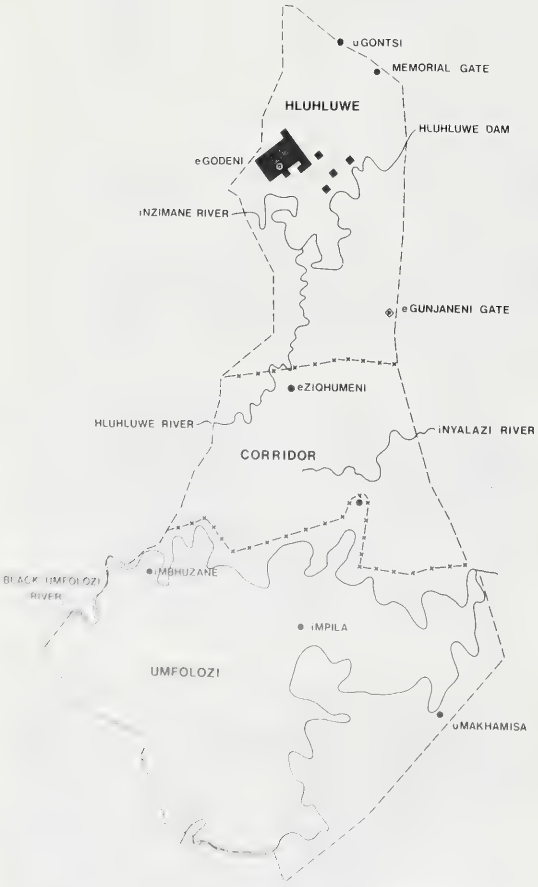

FIG. 1. Map of the Hluhluwe-Umfolozi Complex, showing the approximate position of the proclaimed boundaries of the two [illegible] known distribution of [illegible]

1. From February 1978 to June 1981 research and management personnel working in the Complex were requested to report all alien plant infestations seen in the course of their normal duties. From November 1978 this reporting was facilitated by the use of an Alien Plant Sighting Form (Appendix) which was filled in and returned by officers observing alien plants anywhere in the Complex. Annual Alien Plant Identification lectures were given to the game guards who patrol the Complex extensively.

2. Intensive searches of small areas were made by research staff over the period February to May 1978. In particular the areas surrounding each of 116 permanent vegetation monitoring points located systematically throughout the Complex were searched during March 1978.

3. Alien plants were recorded at 554 points at 200 m intervals along the entire road system in Hluhluwe and the northern Corridor during April 1980.

4. All gardens in the Complex were systematically searched for invasive alien plants during July 1980.

5. Information was obtained from Alien Plant Control Record Forms returned by management staff for completed control operations.

6. Information on the history of the infestations was obtained from herbarium specimens, from records of past control operations lodged in the Hluhluwe Research Centre and from the Hluhluwe Management Plan (Anon., 1975).

All reported infestations over the period 1978 to 1981 were plotted on 1 : 50 000 maps of the Complex using a 500 m by 500 m grid square as the mapping unit. Therefore the distribution maps presented in this paper give an exaggerated impression of the extent of alien plant infestations as many of the grid squares have been shaded on the basis of records of single or scattered plants. This mapping system was chosen as in some areas within the Complex it is difficult to locate an infestation more accurately than as being in a 500 m by 500 m grid. Also the system indicates the rough areas that will require sweeping during control operations if all outlying plants are to be removed.

RESULTS

The species of alien trees, shrubs and creepers that were found to be invading indigenous vegetation are listed in Table 1. The extent of the mapped distribution of each species as well as the number of Alien Plant Sighting Forms returned for each species are also shown to give some relative measure of the magnitude of the different species' invasions of the Complex.

In addition to these 16 species which are propagating themselves in the indigenous vegetation areas of the Complex (termed 'active invaders'), four species (*Acacia mearnsii*, Black Wattle; *Euphorbia pulcherrima*, Poinsettia; *Cereus peruvianus*, Queen of the Night Cactus; and *Musa sapientum*, Banana) were found in areas of indigenous vegetation, either as relics of disused habitation sites or as the result of the dumping of

TABLE 1.—The alien trees, shrubs and creepers found invading indigenous vegetation in the Hluhluwe-Umfolozi Complex, with two measures of the extent of their infestation. 1978–1981*

Species or genus	Local common names (English and Zulu)	Origin	No. of 500 × 500 grid squares in which recorded Feb. 78–June 81	No. of alien plant sighting forms returned Nov. 78–June 81
Agave sisalana	Sisal, uHalibhoma	Mexico	30	5
Caesalpinia decapetala	Mauritius thorn, uFenisi or uLozisi	Tropical Asia	15	16
Cassia didymobotrya	Peanut Cassia, —	Tropical East Africa	7	6
Cassia bicapsularis	Cassia, —	Tropical America	2	3
Chromolaena odorata	Trifid weed, Eupatorium, Sandanezwe	South America	154	84
Citrus limonia	Lemon, Lamula	S.E. Asia	5	2
Jacaranda mimosifolia	Jacaranda, —	South America	6	10
Lantana camara	Lantana, uBukhwebezana	Tropical America	2	1
Melia azedarach	Seringa, uMsilinga	S.W. Asia	88	39
Montanoa bipinnatifida	Montonoa, —	Mexico	5	7
Morus alba	Mulberry, uMbhombe	Asia	3	3
Opuntia spp.	Prickly pear, uMdolofiya	Central America	87	51
Psidium guajava	Guava, uGwava	Tropical America	29	18
Ricinus communis	Castor oil plant, uMhlakuva	?Tropical Africa	56	18
Solanum mauritianum	Bugweed, isiGwayana	Tropical Asia	52	38
Solanum seaforthianum	Potato creeper, uMbangandlala	Tropical America	29	25

* In addition to the above 16 species, 4 species have been found growing around habitation sites, but do not appear to be invading indigenous vegetation except where they have been 'dumped': *Acacia mearnsii,* Black wattle; *Euphorbia pulcherrima,* Poinsettia; *Cereus peruvianus,* Queen of the Night Cactus; and *Musa sapientum,* Banana.

garden refuse which had subsequently rooted and grown (termed 'passive invaders').

Information on the habitat types being invaded by the 16 actively invading species was extracted from returned Alien Plant Sighting Forms (Table 2). This is only an approximation to the actual habitat distribution shown by each species as no correction has been made for the differences in area of the various habitats within the Complex nor for variations in the intensity of searching within each habitat type. However, except for the two *Solanum* species (which are almost certainly commoner in forest and forest edge habitats than along streams and around current habitations as the records suggest) the results are in agreement with the author's subjective assessment of the situation.

These results show that the habitats most susceptible to invasion by alien plants are the riverine habitat followed by closed woodland and forest edge habitats. Undisturbed patches of forest appear able to exclude most of the alien plant species currently occurring in the area. Grassland and open woodland habitats, in which frequent fires occur, are also apparently less susceptible to invasion. Surprisingly, erosion sites were not found to hold extensive infestations of any alien plant species and only three species were recorded in this habitat. Possibly these sites are too xeric for most of the alien plant species occurring in the Complex. The significance of the disturbed ecosystems around current habitations as a source area for the invasion of the surrounding indigenous vegetation is clear. Disused habitation and road verges play a similar role but on a lesser scale. The results of the systematic survey along the roads in Hluhluwe and the northern Corridor (Table 3) indicate the extent of invasions in this portion of the Complex. The frequencies recorded are in agreement with subjective assessments of the extent of the infestations of the various species in this area.

Local sources of infestation

Of the 16 active invader species six (*Agave sisalana, Cassia bicapsularis, Jacaranda mimosifolia, Lantana camara, Montanoa bipinnatifida* and *Solanum seaforthianum*) have all their infestations in the Complex as a result of injudicious plantings of the species as garden plants and, in the case of *Agave sisalana* as a boundary 'hedge'. The four passive invaders (*Acacia mearnsii, Euphorbia pulcherrima, Cereus peruvianus* and *Musa sapientum*) also fall in this category.

A further seven species (*Caesalpinia decapetala, Cassia didymobotrya, Citrus limonia, Melia azedarach, Morus alba, Opuntia* spp, *Psidium guajava*) have also been planted as garden plants in the Complex and at least some of the infestations recorded are the result of these plantings.

In the case of ten of the active invader species, at least some of the infestations have arisen from disseminules entering the Complex from parent plants growing outside its boundaries. These species present management problems that will never be

TABLE 2.—The proportion$^{\times}$ of reported infestations in the different major habitats of the Hluhluwe-Umfolozi Complex

	Major habitat types										No. of habitat reports for each species
	Natural						Man-made				
	Forest	Forest edge	Riverine	Closed woodland	Open woodland	Grassland	Erosion site	Road edge	Disused habitation	Current habitation	
Agave sisalana				,4	,1		,1		,3	,1	7
Caesalpinia decapetala		+	,9							,1	16
Cassia didymobotrya		,1	,3							,6	8
Cassia bicapsularis		,2	,2	,2						,4	5
Chromolaena odorata	,1	,1	,4	,1	,1	+		+		,2	86
Citrus limonia		,1	,2	,1					,1	,5	10
Jacaranda mimosifolia	+	,1		,1						,8	10
Lantana camara										1,0	2
Melia azedarach		+	,9			+			+	,1	44
Montanoa bipinnatifida		,1					,1			,8	8
Morus alba			,8							,2	4
Opuntia spp.			,7	,2	,1				+	+	52
Psidium guajava		,1	,2	,1	,1	,1		,1	+	,3	18
Ricinus communis			,9					+		,1	16
Solanum mauritianum	,1	,2	,4			+	+	+		,3	39
Solanum seaforthianum	,2	,2	+	,1				+		,5	22
Mean rating over all species	,025	,075	,369	,081	,025	,006	,012	,006	,025	,375	
Number of species	4	11	12	8	4	4	3	5	5	16	

+ = proportion less than ,05 or known to occur, but not reported on any form

× = all proportions have been rounded to sum to 1,0 for each species; rounding has in some cases been subjective and has been done so as to approximate more closely the intensity of infestations observed in different habitats.

completely solved until suitable buffer zones in surrounding areas are cleared of the species.

Individual species accounts

Agave sisalana, *Cassia bicapsularis*, *Citrus limonia*, *Lantana camara* and *Montanoa bipinnatifida* have all been observed to disperse only a short distance from their parent plants in the Complex. Total eradication appears possible given an adequate labour input over several years.

Jacaranda mimosifolia and *Solanum seaforthianum* have both only invaded indigenous vegetation in northern Hluhluwe from parent plants initially planted in the eGodini gardens.

Jacaranda mimosifolia was planted at a minimum of four outposts in the Complex, the earliest plantings being at Masinda and eGodeni, the latter in the late 1940's. By 1972 plants of this species were found [illegible]ion up to 2 km from the eGodini gardens. In the same year control operations in an area of approximately 40 ha around the eGodini gardens revealed a mean density of 300 seedlings and saplings/ha and their removal required approximately 16 manhours/ha (Anon., 1975: 39).

TABLE 3.—Frequency of occurrence of alien plants at 554 points systematically located at 200 m intervals along the entire road system in Hluhluwe Game Reserve and the northern Corridor. April 1980.

Species	Number of points at which the species was recorded
Chromolaena odorata	13
Solanum mauritianum	7
Solanum seaforthianum	5
Ricinus communis	4
Psidium guajava	3
Agave sisalana	2

Following the discovery of the invasion threat posed by *J. mimosifolia* strenuous efforts were made to remove all the individuals of this species from gardens. The species proved difficult to kill but complete eradication from garden areas should be achieved by 1982. Future control will consist of 'mopping-up' operations to remove individuals surviving in the surrounding indigenous vegetation.

The invasion of indigenous savanna and forest vegetation in southern Africa by *J. mimosifolia* has now been documented in several studies (e.g. Drummond, 1975; Petheram, 1979; Wells *et al.*, 1979). This species should never again be planted in a protected area.

Solanum seaforthianum is bird dispersed and its invasion of indigenous vegetation around eGodini has been extensive (Fig. 1). In some patches of low canopy forest on eGodini the relatively unpalatable *S. seaforthianum* was one of the dominant understory species by 1978. Intentional cultivation of this creeper in gardens was finally eliminated in 1980. However, by this time, fruiting was occurring so extensively in adjacent areas of indigenous vegetation that reinvasion of gardens is an ongoing problem.

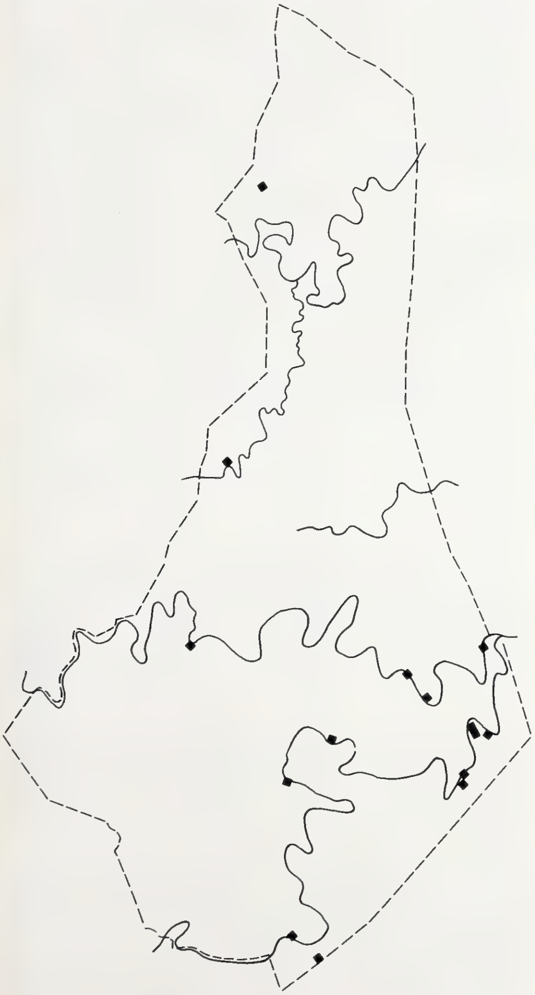

FIG 2.—The known distribution of *Caesalpinia decapetala* in the Complex, 1978–1981.

This species has shown itself capable of invading indigenous vegetation elsewhere in south east Africa (Ross, 1972: 309; Biegel 1977: 99; Ndumu Game Reserve, Natal, pers. obs.; Mkuzi Game Reserve, Natal, P. S. Goodman, pers. comm.). Its major impacts are likely to be competition for light, water and nutrients with other forest and forest edge species and for dispersal vectors with indigenous, bird distributed, plant species. Plants are often widely scattered and hand removal using lines of labourers sweeping infested areas appears the only practical control method. Repeated removal operations are necessary; in one case an area cleared in 1978 had been reinvaded to a density of 2 750 plants/ha by June 1979, when it was recleared, after which it was reinvaded to a density of 1 225 plants/ha by June 1981.

Caesalpinia decapetala is grown extensively as a hedge in adjacent farming areas where it has invaded indigenous vegetation. Fortunately it has only once been planted in a garden on eGodini from where it apparently has not spread. As a result of confusion with indigenous thorny creepers, e.g. *Entada spicata* and *Acacia schweinfurthii,* infestations of this species along the banks of the major inflowing rivers (the Hluhluwe, Black and White Umfolozi Rivers) were not detected until 1979 (Fig. 2). Extremely costly to remove and capable of massive seedling establishment (Petheram, 1979) this species forms impenetrable thickets which could have a major impact on the riverine areas of the Complex.

Cassia didymobotrya has been planted in gardens in and around the Complex and in adjacent farming areas has invaded indigenous vegetation extensively. Inside the Complex it has only been found invading indigenous vegetation in a limited area around the eGodini gardens and along the banks of the inflowing Nzimane River. First recognized as being an alien in 1978 *C. didymobotrya* has now been removed from all gardens in the Complex. Currently it is a minor threat but one that will require constant vigilance along influent rivers.

Chromolaena odorata is the most widespread alien invader in the Complex (Fig. 3) and is the alien plant currently posing the most serious threat to the long term maintenance of natural vegetation within the area. It is wind dispersed and capable of extremely rapid growth to form impenetrable tangles which eventually shade out all the indigenous vegetation. A particularly dangerous attribute of *C. odorata* is the plant's high flammability: it burns even when green in midsummer. The species forms dense thickets on the edge of forest and riverine forest, ecotones which are normally fire excluding. Following invasion by *C. odorata* fires burning in adjacent grassland and woodland areas cross this ecotone with ease and burn right into the canopies of fire sensitive forest trees. *C. odorata* coppices readily following fire and the bare areas formed after a thicket has burnt out provide suitable germination conditions for this species.

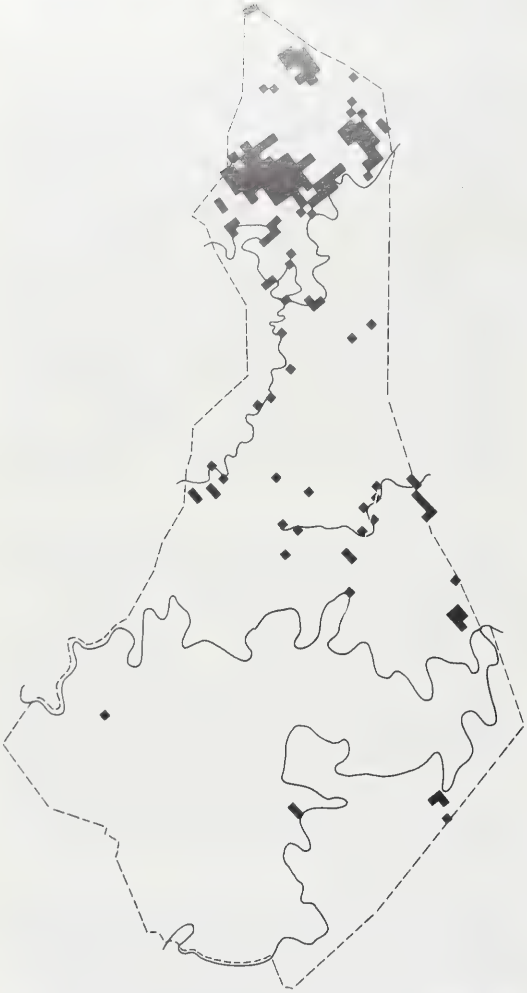

FIG 3.—The known distribution of *Chromolaena odorata* in the Complex, 1978–1981.

The conditions prevailing in northern Hluhluwe Game Reserve appear to be optimal for this species: a specimen with a basal stem diameter of 24 cms was removed from a forest edge infestation in 1978. Densities in excess of 48 000 plants/ha have been measured both from a riverine infestation in the south eastern Corridor in 1978 and, in 1981, from an area in Hluhluwe that had previously been 'cleared' of *C. odorata* on two occasions since 1977. A patchy infestation along a forest edge at eGodini covering some 83 ha had a mean density of 4 010 plants/ha and required an input of 47 manhours/ha for complete removal using mattocks and hand pulling. An extremely dense established thicket on a forest edge took 630 manhours/ha using the same methods.

First recorded in Hluhluwe in 1961, the species is just beginning the 'exponential' phase of its population increase in the Complex. Increases in the distribution and density of the species in Hluhluwe since 1978, in spite of an increased control effort, make the future prospect extremely bleak.

Already this species has had a massive deleterious effect on indigenous vegetation throughout the subtropical areas of Natal. Virtually all the protected areas in the region have already been invaded, some have been swamped e.g. Krantzkloof Nature Reserve. It is a matter of time before all the protected areas are invaded. It seems likely that the species, if unchecked, will continue its northward spread into Mozambique, the Eastern Transvaal and Zimbabwe.

The discovery of a biological control method for *C. odorata* is essential if the natural ecosystems occurring in the subtropical portion of Natal, and possibly further afield, are to be conserved.

Melia azedarach has in the past been intentionally planted in some of the gardens in the Complex. However, this error was soon recognized and efforts were first made to eliminate this species from gardens in 1963. By this time mature plants were established in surrounding areas of indigenous vegetation and reinvasion of gardens from this source is still occurring. The major infestations of this species now occur on the banks of the inflowing

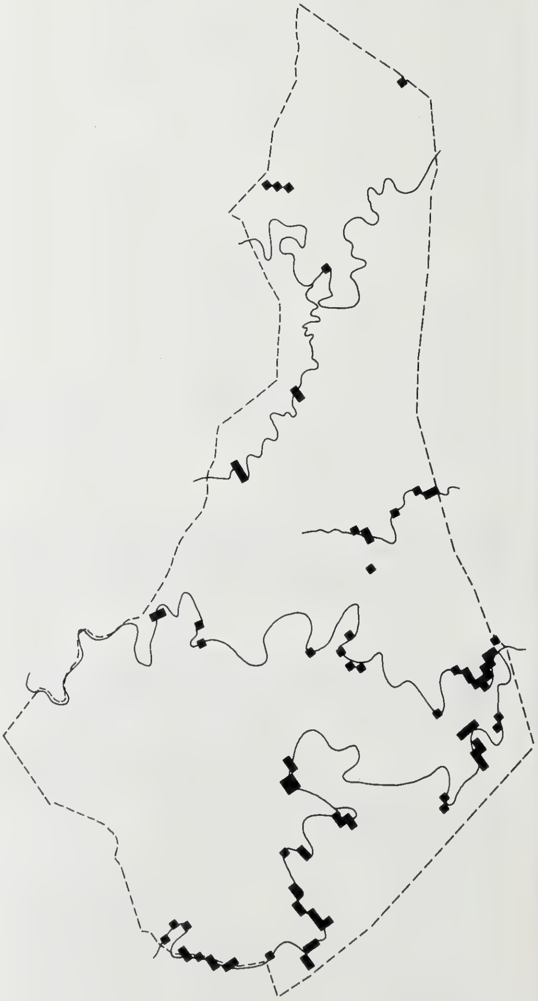

FIG 4.—The known distribution of *Melia azedarach* in the Complex, 1978–1981.

rivers (Fig. 4), in particular the Hluhluwe and Umfolozi Rivers. There is an independent infestation along the Nyalazi River that rises inside the Complex, presumably these plants arose from seed dispersed from the Masinda outpost which was only cleared of *M. azedarach* in 1975.

In addition to being bird dispersed, it appears that the seeds are transported by water (cf. Van Wyk, 1972: 267) and major infestations are present on river bends where flood waters periodically inundate riverine *Phragmites* reed beds and *Ficus sycamorus* riverine forest. At Makhamisa on the White Umfolozi River in August, 1978, *M. azedarach* was present at a density of 120 trees/ha in a community where all the indigenous tree species had a combined density of only 105 trees/ha. At this locality *M. azedarach* contributed 4,94 m^2/ha to a total basal area of 14,55 m^2/ha for the entire tree community.

This species has shown itself capable of outcompeting indigenous vegetation in various localities throughout the naturally wooded regions of southern Africa (Van Wyk, 1972: 267; Palgrave, 1977: 381; Petheram, 1979; Wells *et al.*, 1979). The tree is long lived and can grow to a considerable size (10 to 15 m in height and canopy spread) and therefore has the potential to radically distort indigenous plant communities. That the community particularly threatened within the Complex is the riverine fringe, which is a community of limited extent (52,7 km^2 of the 900 km^2 area) and of critical significance to a wide variety of the area's fauna, makes the situation particularly serious.

As the species produces a large crop of fruits each year which persist on the tree for a long period and are avidly eaten by a wide range of frugivorous birds it is possible that uncontrolled infestations of this species could give rise to vector competition with less favoured indigenous fruiting species. In this respect, I have observed both Brown-necked parrots *Poicephalus robustus* and Rameron pigeons *Columbia arquatrix* leaving their normal forest haunts in the Natal midlands to visit fruiting *M. azedarach* trees growing in open grassland and thornveld situations.

The problem status of the species is exacerbated by its high germinability, rapid growth and the extreme difficulty with which established individuals can be killed. Wells *et al.* (1979) working in the central Transvaal found that *M. azedarach* 'is undoubtedly the most aggressive exotic, woody invader encountered'.

In the interests of conservation, it is time that this species was declared a noxious weed throughout the Republic of South Africa and research into its biological control should be initiated immediately.

Morus alba has also been grown in gardens in the Complex and it was only following its discovery as an invader of riverine forest along the White Umfolozi River in 1979 that its cultivation within the Complex was prohibited. Known to have invaded indigenous vegetation elsewhere in southern Africa (Palgrave, 1977: 100; Wells *et al.*, 1979) this species should not be cultivated in protected areas. Control of this species in the Complex is currently a minor problem.

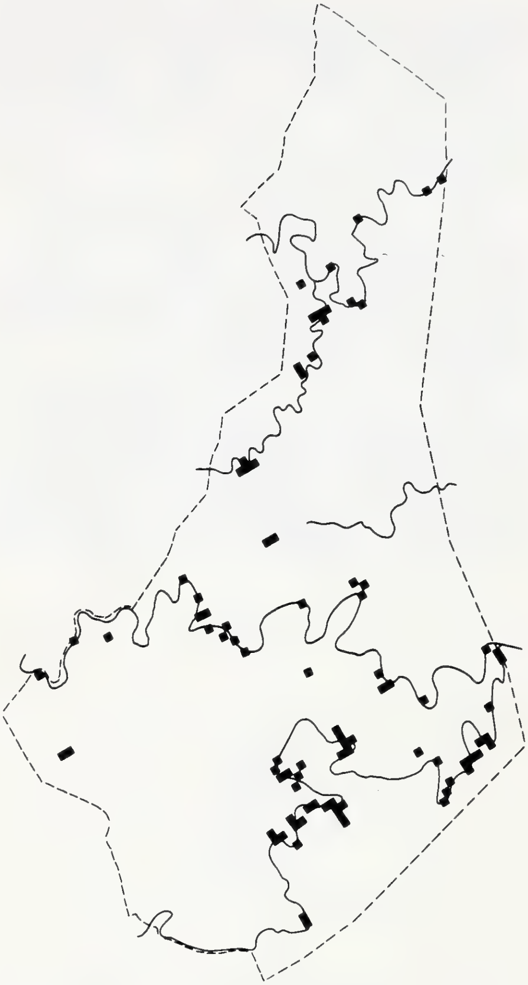

FIG 5.—The known distribution of *Opuntia* spp. in the Complex, 1978–1981.

Opuntia spp. have been found scattered throughout the Complex (Fig. 5) with the banks of the major inflowing rivers holding the highest density of infestations. Most of the infestations reported were of established plants forming clumps less than 100 m^2 in area. Many of the infestations have been known for years, have been subjected to repeated unsuccessful or only partly successful control operations and do not appear to be spreading rapidly. Only along the rivers, where cladodes are apparently deposited by flood waters, were young infestations found.

This species is considered to have been first introduced during the Nagana campaign (approximately 1930 to 1963) and a number of infestations are at old Nagana camps. *Opuntia* spp. were the first alien plants to be controlled in the indigenous vegetation areas of the Complex (1963 in Hluhluwe and 1967 in Umfolozi). Most of the control operations have involved physical removal of the plants, with a number of herbicide treatments also having been tried. In 1974 the biological control agent, cochineal *Dactylopius opuntiae*, was introduced into some of the larger infestations in Umfolozi, but has failed to control these completely. The cochineal is apparently unable to reach all the scattered infestations and, of forty infestations for which its presence or absence was recorded, only five were infected, of which one was the site of an original introduction in 1974.

These species are known to form dense thickets where not controlled (Henderson & Anderson, 1966: 220; Stirton, 1978: 112) and their potential impact on the Complex is serious. An effective control strategy, based on the recent research conducted in the eastern Cape, should be implemented as soon as possible.

Psidium guajava is also a species that was introduced, in ignorance of its invasive potential, to numerous gardens in the Complex. However, it has invaded indigenous vegetation throughout the Natal coastal belt and it is unlikely that all the present infestations in the Complex are the result of garden introductions, although the worst area is that surrounding the eGodini gardens (Fig. 6).

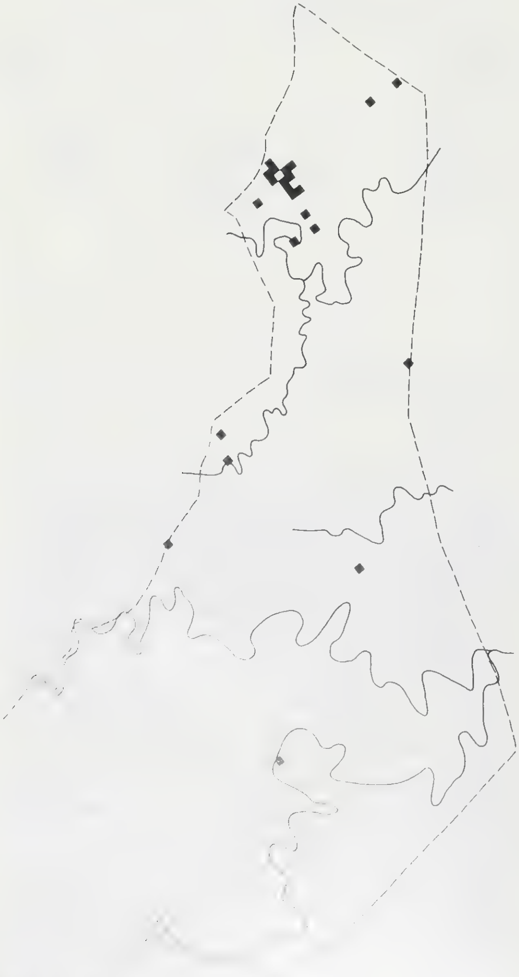

Fig. 6.—The [illegible] distribution [illegible] *Psidium guajava* in the Complex, [illegible]—1981.

This species is an extremely dangerous alien being able to outcompete indigenous vegetation over a wide range of habitats in Natal, Eastern Transvaal and Zimbabwe (Drummond, 1975). The invasion of the Natal coastal belt is already extensive and in the Ndumu Game Reserve the species now dominates the dryland fringe of the riverine forest along the Pongola River. The habitats most threatened in the Complex are the forest edge and riverine fringe.

Fortunately, control operations, initiated in 1970 in Hluhluwe and in 1975 in Umfolozi, have greatly limited the fruiting of this species in the Complex. *P. guajava* has proven almost impossible to kill. All the herbicides tested so far have failed. Physical removal is only partly successful as the species suckers readily from root remnants. Research into an effective control method is essential if the species is to be controlled indefinitely.

P. guajava is another species that should never again be intentionally introduced to a protected area.

Ricinus communis is now so widespread in indigenous vegetation in Natal that many people have assumed that this alien is in fact indigenous. The first known record of the species in the Complex is a collection made by C. J. Ward in 1955 when its distribution was 'localized'. The species was not subjected to control operation till 1978, although its cultivation in gardens was prohibited from 1972. *R. communis* is still localized to areas of disturbed soil along rivers, roads and around habitation (Fig. 7). It does not seem to be able to invade indigenous vegetation except where this has been artificially disturbed. Its only significant impacts would appear to be through competition with indigenous ruderals, particularly on recently exposed silt deposits along riverbanks and in dry riverbeds, and through its alteration of the natural feeding ecology of doves, particularly Tambourine doves *Turtur tympanistria* (McLachlan & Liversidge, 1978: 230). If uncoltrolled, large infestations of this species could alter the feeding ecology of these birds.

Solanum mauritianum is present mainly in the moister northern parts of Hluhluwe with scattered individuals recorded from river banks and habitation sites further south in the Complex (Fig. 8). The first record of this species from the Complex is a collection made in Hluhluwe by P. Hitchins in 1971 when it was said to be 'frequent' in occurrence. Photographs taken in 1949 of a site on eGodini which was heavily infested by 1978 showed *S. mauritianum* to be absent at this date. The species was not subjected to control operations till 1978 although its cultivation in gardens was prohibited in 1972.

S. mauritianum is an aggressive invader of forest edge communities, particularly where these are disturbed (Henderson & Anderson. 1966: 278) and by 1978 dense infestations were present in these situations throughout the eGodini area of Hluhluwe.

S. mauritianum is bird distributed, germinates readily, grows rapidly and can form dense stands up to 5 m in height which preclude indigenous forest

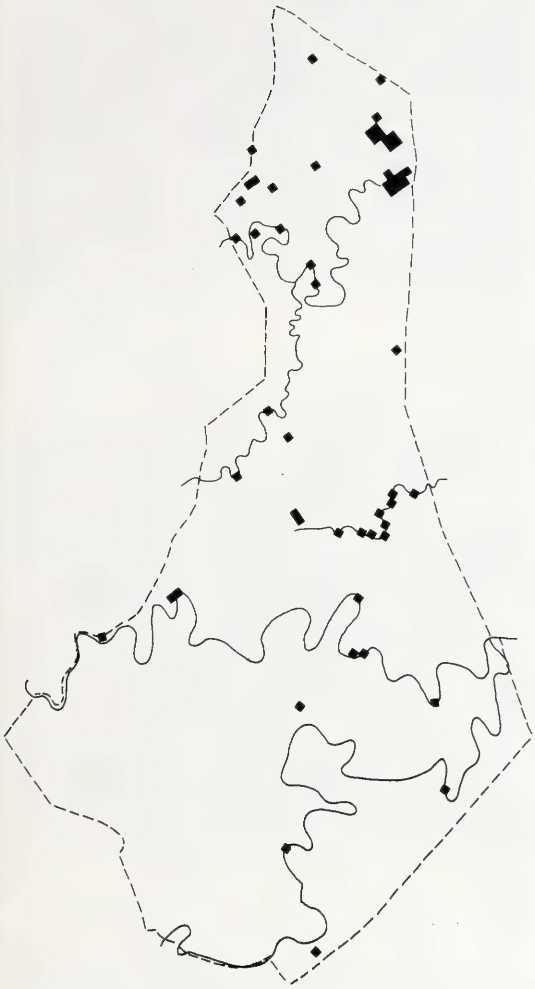

FIG 7.—The known distribution of *Ricinus communis* in the Complex, 1978–1981.

edge plants such as *Trema orientalis,* an important species for avian frugivores, and *Dombeya burgessiae,* an important species for honey bees. Individuals of *Solanum mauritianum* are relatively long-lived reaching basal stem diameters in excess of 15 cm without showing any signs of senescence.

The possible indirect effects of the invasion of forest edge habitats by this species are numerous: Its fruits which it produces prolifically all the year round are eaten avidly by most indigenous avian frugivores. Already these fruits have radically altered the feeding ecology of the Rameron pigeon *Columba arquatrix* in the Natal Midlands (Oatley, 1980) and this could have serious consequences for indigenous forest plants which were formerly dispersed by this species (Phillips, 1927). The foliage of *Solanum mauritianum* is not eaten by indigenous ungulate browsers in the Complex, the forest species of which feed extensively in edge situations. Dense infestations of *S. mauritianum* could significantly reduce browse availability for these species. Already it has been observed that the Bushbuck *(Tragelaphus spekei)* population in the eGodini area of H. G. R. has declined markedly since the 1950's and, although there are several possible explanations for this decline, the increase in *Solanum mauritianum* infestations might have been a contributory factor.

Control measures

The following actions have been taken to eliminate or reduce the threat posed by alien plants in the Complex:

1. All alien plants, excluding a small list of selected "permissible" species are being phased out of gardens in the area. No further introductions of any new alien plant species to these gardens is allowed. A policy of growing only species indigenous to the Complex is being actively encouraged (Macdonald *et al.,* 1979).

2. The introduction of a continuous monitoring system using the Alien Plant Sighting Form (Appendix) enables control operations to be implemented on the basis of the most up to date information available on the distribution and extent of infestations.

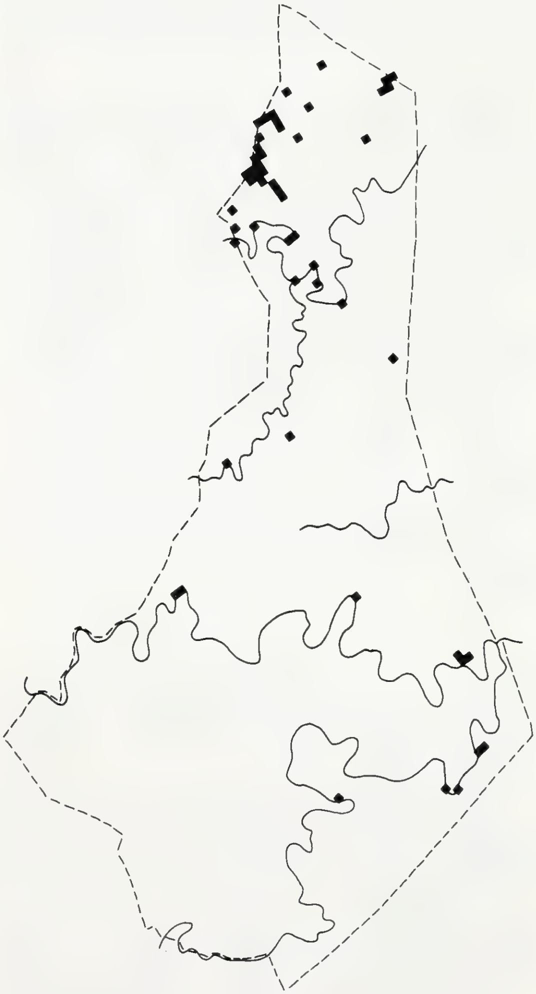

FIG 8.—The known distribution of *Solanum mauritianum* in the Complex, 1978–1981.

3. All alien plant control operations in the Complex have now been put on a systematic basis with an annual planning meeting being held at the start of each year. All completed control operations are recorded on Alien Plant Control Record Forms which will enable the efficiency of these operations to be evaluated and, hopefully, improved.

4. A greatly increased financial allocation has been made for alien plant control work.

5. The alien plant species have been ranked in the following order of priority for control operations: *Chromolaena odorata, Melia azedarach, Psidium guajava, Caesalpinia decapetala, Solanum mauritianum, Lantana camara* (due more to its potential threat than to its currently realised threat), *Opuntia* spp., *Solanum seaforthianum, Cassia didymobotrya, Jacaranda mimosifolia, Morus alba, Ricinus communis, Montanoa bipinnatifida, Citrus limonia, Cassia bicapsularis, Agave sisalana, Acacia mearnsii, Cereus peruvianus, Euphorbia pulcherrima* and *Musa sapientum.*

6. Further trials have been initiated on the chemical control of some of the alien species that have proven difficult to kill e.g. *Caesalpinia decapetala, Chromolaena odorata* and *Melia azedarach.*

One general point needs to be made relating to the urgency with which the control of some of these alien plants needs to be undertaken. During the course of this survey it was noted that plants of *Chromolaena odorata, Jacaranda mimosifolia, Melia azedarach, Opuntia* spp. *Solanum seaforthianum* and particularly *Lantana camara* were being controlled to some extent by browsing. In the case of *L. camara* plants growing outside gardens this control was absolute. Infestations of *C. odorata* were also often severely defoliated by browsers (18 out of 33 infestations for which the presence or absence of natural control was recorded). Large scale reductions in the populations of two of the most important browsers, nyala (*Tragelaphus angasi*) and impala (*Aepyceros melampus*), are currently being undertaken throughout the Complex for conservation reasons. Thus this natural control through browsing could well be significantly reduced in the years to come.

CONCLUSIONS

The threat posed by alien trees, shrubs and creepers to the longterm maintenance of natural ecosystems in the Complex is much more serious than was realized in the past.

The following actions should be taken to reduce the threat posed by alien plants to the ecosystems conserved in the Complex as well as to those elsewhere in Natal.

1. Biological control techniques should be developed for the control of *Chromolaena odorata* and *Melia azedarach* as a matter of urgency.

2. Both the above species should be declared noxious weeds throughout the republic of South Africa. The current situation whereby a garden enthusiast could intentionally introduce *Chromolaena odorata* to, say, the Eastern Transvaal is intolerable. If the controlling authorities of land outside the protected areas of Natal are not forced to control infestations of these two species on their land the protected areas will be fighting a never ending battle to control infestations within their boundaries. The damage these two species are causing to indigenous vegetation in both the protected and unprotected areas of Natal is already so great that our failure to act decisively against them now will be considered a dereliction of duty by future generations.

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APPENDIX

ALIEN PLANT SIGHTING FORM

SPECIES: ....

GRID SQUARE: .. ..

GRID QUARTER: ________

N.B. (1) Note each infestation and each species on a separate form

(2) Note all infestations you have not reported this year

(3) Indicate the appropriate categories by placing an 'X' in the space provided.

RELOCATION INSTRUCTIONS: ....

....

....

HABITAT: Forest .... Forest edge .... Riverine .... Closed woodland .... Open woodland .... Grassland .... Road edge ....

Old habitation .... Current habitation .... Erosion site .... Other (specify) ....

DID YOU REMOVE THE INFESTATION? Yes .... No ....

INFESTATION DETAILS

(1) AREA: ....m X ....m OR ....ha OR ....m of riverine strip infested — Measured .... Estimated ....

(2) NUMBER OF PLANTS: .... in total OR .... per unit area (m² or ha) OR .... per unit length of riverine strip infested. — Measured .... Estimated ....

(3) HEIGHT OF PLANTS: Maximum ....m, Mean ....m. — Measured .... Estimated ....

(4) BASAL STEM DIAMETERS: Maximum ....cm, Mean ....cm. — Measured .... Estimated ....

(5) REPRODUCTIVE STATE: Offspring present .... Signs of previous fruiting .... Currently flowering .... Currently fruiting ....

Considered to be of reproductive size .... Not yet reproductive size ....

(6) NATURAL CONTROL: Are the plants showing signs of being controlled naturally? — Yes .... No ....

If so specify means (i.e. inundation, browsing, disease, etc.) ....

(7) PREVIOUS CONTROL: Are there signs of previous control operations? — Yes .... No ....

If so (a) what percentage of treated plants have been killed? ....% — Measured .... Estimated ....

(b) are the living plants now mostly coppicing .... suckering from roots .... or seedlings ....

(c) does the regrowth from treated plants appear to be unhealthy? — Yes .... No ....

(8) FUTURE CONTROL: How many labourers (........) working for how many days (........) do you estimate would be required to control the infestation using what method (..)?

Date observed: .... Date completed form: ....

Observers name: .... Compiler's name: .... (where different)

To your knowledge has this infestation been reported on in previous years? Yes .... No ....

Bothalia 14, 3 & 4: 961–965 (1983)

Weed flora of South Africa 2: power shifts in the veld

M. J. WELLS*, V. M. ENGELBRECHT**, A. A. BALSINHAS* and C. H. STIRTON*

ABSTRACT

This paper, the second in a series analysing data from the National Weed List, concentrates on weedy changes that affect the indigenous flora. The incidence of weediness and of threatened species is used as an indication of success or failure of families under prevailing conditions of disturbance. The resulting power shifts between indigenous families and the impact of exotic weeds on the situation are reviewed.

Many power shifts are taking place between indigenous species in the veld. Superficially it seems as though a relatively few invasive species are displacing a larger number of threatened species, but evidence from Natal points to more species increasing than decreasing under conditions of over-utilization.

Amongst small families power shifts are almost as prevalent and important as at species level. Seventeen small families have over 20% indigenous weed species. Thirty small families have over 20% threatened species, and 21 small families have had their species numbers bolstered by more than 20% by exotic weeds.

A very few large and medium-sized families contain over 50% of our weeds and our threatened species. It is mostly temperate (Cape) families that are under pressure relative to more tropical families. This trend is echoed at sub-family level within the Fabaceae.

RÉSUMÉ

LA FLORE DES PLANTES NUISIBLES D'AFRIQUE DU SUD 2: LEUR AGRESSIVITE DANS LE VELD

Ce document, le second d'une série analysant les données de la Liste nationale des Plantes Nuisibles, a trait à la substitution de la flore indigène par les plantes nuisibles. La présence relative des plantes nuisibles et des espèces menacées donne une indication sur la vitalité ou non des familles dans les conditions actuelles de perturbation. Les changements de dynamisme qui en résultent parmi les familles indigènes et l'impact des plantes nuisibles exotiques sur cette situation sont passés en revue.

Le dynamisme de nombreuses espèces indigènes du veld est en train de se modifier. A première vue, il semble qu'un grand nombre d'espèces menacées sont remplacées par un nombre relativement restreint d'espèces envahissantes, mais l'expérience acquise au Natal montre un accroissement plutôt qu'une diminition du nombre d'espèces dans des conditions d'agriculture intensive.

Les changements de dynamisme sont pratiquement aussi important au niveau des petites familles qu'au niveau spécifique. Dix-sept petites familles comptent plus de 20% d'espèces de plantes nuisibles indigènes. Trente petites familles comptent plus de 20% d'espèces menacées et vingt et une petites familles ont vu leur nombre d'espèces s'accroitre de plus de 20% de plantes nuisibles exotiques.

Très peu de familles de moyenne et de grande importance contiennent plus de 50% de nos plantes nuisibles et de nos espèces menacées. Ce sont surtout les familles tempérées (du Cap) qui sont menacées, camparées aux familles tropicales qui sont plus nombreuses. Cette tendance se retrouve au niveau de la sous-famille chez les Fabacées.

1 INTRODUCTION

The veld, that 'ragged-brown carpet, vast and bare', that has served South Africa so well for so long is now becoming threadbare, leaving the way open to invasive weeds (Fig. 1).

Three main types of invasion by indigenous species take place (Wells & Stirton, 1981):

— On its higher, drier margins the retreating grassland is being invaded by small, xerophytic 'karroid' shrubs. This is referred to as the spread of the karoo.

— On its lower, moister margins grassland is being invaded by trees (followed by shrubs and herbs) from the adjacent wooded communities. This is referred to locally as 'bush encroachment'.

— In the heart of the grassland, particularly on the higher, wetter ridges, unpalatable grassland species, including tussocks and poisonous plants are on the increase.

These power shifts between physiognomically distinct communities are individually well known (Acocks, 1975), although it is doubtful if there is sufficient appreciation of their cumulative effect on the vulnerable grassland biome.

Power shifts between taxa, between exotics and indigenous plants, and between plants with different life cycles often take place within physiognomically homogeneous communities. Unless the plants involved are very distinctive, e.g. *Aloe* species increasing at the expense of grasses, these changes tend to go unnoticed. A case in point is the gradual infiltration of streambank communities by woody exotics, which has resulted in the almost total replacement of indigenous woody, streambank species in many places (Wells *et al.*, 1980; Duggan *et al.*, 1981).

In this paper we will try to throw more light on changes being brought about in the South African

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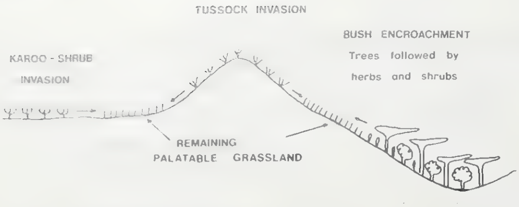
TUSSOCK INVASION
KAROO - SHRUB INVASION
BUSH ENCROACHMENT
Trees followed by herbs and shrubs
REMAINING PALATABLE GRASSLAND

FIG. 1.—Diagrammatic representation of the three main types of invasion of the grassland.

flora as a result of weed invasion, and to answer the questions:

— 'What power shifts are taking place between indigenous vascular plant taxa?' and

— 'How are exotics affecting the situation?' To answer these questions we need to know not only what taxa are showing expansionist tendencies, but also which are giving way. In the absence of specific and wholly compatible data on the subject, we have taken:

— inclusion in the National Weed List (Balsinhas *et al.*, in press) as an indication of maintained or increasing success; and

— inclusion in lists of threatened species (Hall *et al.*, 1980; Arnold *et al.*, unpubl.) as an indication of lack of or decreasing success.

2 POWER SHIFTS BETWEEN TAXA

Power shifts have been analysed at species and at family level.

2.1 *Species level*

At present, of the 20 044 species of indigenous vascular plants recognized in South Africa:

— 879 (4,4%) are regarded as weeds, including 485 (2,4%) weeds of natural pastures;

— 2 347 (11,7%) are regarded as threatened; and the remaining

— 16 818 (83,9%) have not been placed in either category, and presumably fall somewhere inbetween.

2.1.1 *Indigenous weed species*

Some of the weeds of natural pastures have been so classified because they are poisonous or carry burs, rather than because they are invasive and contribute to power shifts.

There is even one species, *Harpagophytum procumbens* (the grapple plant), a classic weed, that could soon be on the threatened plant list, as a result of over-utilization for medicinal purposes. However, most of the indigenous weeds of natural pastures are woody, unpalatable species that are increasing their range and numbers as a result of disturbance.

In some cases a single species, such as the unpalatable *Aristida junciformis* (ngongoni) replaces not only the previous dominant *(Themeda triandra)*, but supresses most other indigenous plants in the area, forming almost pure stands over thousands of hectares (Edwards *et al.*, 1980). In this particular case, the power shift is serious because it is difficult to reverse by means of management techniques.

In other cases e.g. *Chrysocoma tenuifolia* (the bitter karoo bush) the invasive species are regarded as weeds because they are unpalatable, or even poisonous, but they spread by colonizing bare areas rather than by suppressing other species. They therefore also have a caretaker rôle, providing shade and shelter, binding the soil and acting as a buffer against degeneration (Acocks, 1971). Most power shifts involving caretaker species can be reversed fairly easily using management techniques, provided that the environmental conditions have not degenerated too far.

2.1.2 *Threatened species*

Some of these species are naturally rare or localized and even those whose numbers are decreasing are not all the victims of plant invaders. However, the vigour and adaptability of other plants in the vicinity (even caretaker species) must contribute to the competitive pressures exerted on those that are less resilient.

At present far more indigenous species are considered to be threatened (Hall *et al.*, 1980; Arnold *et al.*, 1980) than are considered to be weeds (Balsinhas *et al.*, 1982). Superficially, it would appear that a relatively few vigorous, invasive, indigenous species are strengthening their positions at the expense of a much greater number of species that either are or will become threatened. In view of this, the lack of knowledge about so many species, their success rate and status, gives cause for concern.

2.1.3 *The species inbetween*

Information about the success or failure rate of species that are neither considered to be weeds, nor threatened, is very fragmentary. Foran *et al.*, (1978) have developed a method for assessing conditions in grassland which measures decreaser species that decline in abundance with bad management, increaser-I species which increase with under-utilization and increaser-II species which increase with over-utilization. Tainton *et al.*, 1978 suggest the addition of an increaser-III group to include species encouraged by selective grazing. Westfall (1981) has expanded the method to include woody vegetation, and there is a good prospect that increaser and decreaser species will be recorded on a countrywide basis during the course of a natural resources survey which is being carried out by the state Department of Agriculture & Fisheries (Edwards, 1981).

It is of interest that Foran *et al. (l.c.)*, recorded more increaser than decreaser species under conditions of over-utilization and the overall effect of power shifts between indigenous species is far from clear.

2.1.4 *Exotic weed species*

Indigenous weeds have been supplemented by 694 exotic weed species, of which 481 are naturalized in the veld and compete directly with indigenous species. Many of these, such as: *Acacia saligna* (Port Jackson wattle), *Hakea sericea* (silky hakea), *Lantana camara* (tickberry), *Opuntia ficus-indica* (prickly pear), *Pinus pinaster* (cluster pine), *Prosopis glandulosa* (mesquite) and *Stipa trichotoma* (nassella tussock) form closed stands excluding

TABLE 1.—The families that supply most of our indigenous species, weeds and threatened species

*Families which between them contain approximately 50% of the species	All indigenous species	Indigenous weed species	Indigenous natural pasture weed species	Indigenous threatened species	Exotic naturalized (flora weed) species	All exotic weed species recorded in South Africa
Mesembryanthemaceae	2527*	9	8	73	0	0
Asteraceae	2115*	133*	100*	187*	53*	90*
Fabaceae	1522*	83*	54*	91*	66*	74*
Liliaceae	1006*	28*	25*	141*	0	3
Iridaceae	811*	15	8	227*	0	0
Poaceae	809*	155*	36*	67	101*	120*
Ericaceae	782*	0	0	92*	0	0
Asclepiadaceae	702*	6	5	118*	1	3
8 Families* supply	**10274***					
out of total of	**20044**					
indigenous species						
Cyperaceae	455	63*	26*	1	0	3
5 Families* supply		**464***				
out of total of		**879**				
indigenous weed species						
Rubiaceae	237	19	17*	15	1	4
6 Families* supply			**259***			
out of a total of			**485**			
indigenous natural pasture weed species						
Proteaceae	365	0	0	140*	6	6
Orchidaceae	466	1	0	118*	0	0
Santalaceae	176	2	2	79*	0	0
9 Families* supply				**1182***		
out of a total of				**2347**		
indigenous threatened species						
Solanaceae	71	13	9	1	21*	31*
4 Families* supply					**241***	
out of a total of					**481**	
exotic flora weed species						
Brassicaceae	111	6	2	47	9	25*
5 Families* supply						**340***
out of a total of						**694**
all exotic weed species						

entire communities of indigenous plants (Stirton, 1978).

2.2 *Family level*

Of the 227 indigenous vascular plant families in South Africa: 156 families (69%) supply 1 000 (5%) of the species; 63 families (27%) supply 8 770 (44%) of the species; 8 families (4%) supply 10 274 (51%) of the species.

2.2.1 *Small families*

The 156 small families contain an average of only 6,4 indigenous species each, and include 46 families with only a single indigenous species. In such small families the success or failure of a single species or a very few species has a profound effect on the fortunes of the family. Power shifts are almost as prevalent and important as they are at species level.

TABLE 2.—The distribution of weeds and threatened species in the three sub-families of the Fabaceae

Sub-family	(A) Total indig. spp.	Indig. weed spp.		(D) Threatened spp.	Exotic weeds		(G) Total change C + D + E in veld
		(B) Total	(C) Natural pastures		(E) Flora weeds	(F) Total	
Caesalpinioideae	53	12 (23%)	8 (15%)	5 (9%)	11 (21%)	12 (23%)	24 (45%)
Mimosoideae	76	25 (33%)	25 (33%)	13 (17%)	17 (22%)	23 (30%)	55 (72%)
Papilionoideae	1 393	45 (3%)	20 (1%)	73 (5%)	31 (2%)	39 (3%)	124 (9%)
Total (Fabaceae)	1 522	82 (6%)	53 (3%)	91 (6%)	59 (4%)	74 (5%)	203 (15%)

There are 17 small families that contain over 20% indigenous weed species. They include the water-plant families: Lemnaceae, Hydrocharitaceae, Potamogetonaceae and Aponogetonaceae, whose species are taking advantage of habitats provided by man-made dams as well as the enriched conditions in natural water bodies.

Thirty of the small families contain over 20% threatened species. These include Rhizophoraceae (50%), Penaeaceae (52%), Arecaceae (67%), and 12 single-species families.

In twenty-one of the small families naturalized exotics have bolstered the species present by more than 20%. These include: the water-plant families Lemnaceae (27%), Hydrocharitaceae (27%), Azollaceae (100%) and Hydrophyllaceae (100%); and terrestrial plant families such as Onagraceae (27%), Passifloraceae (29%), Nyctaginaceae (31%), Plantaginaceae (44%), Myrtaceae (48%), Phytolaccaceae (50%), Salicaceae (71%) and Cactaceae (1 700%).

2.2.2 *Large and medium-sized families*

A very few families supply most of our weeds and threatened species (see Table 1).

Of the 8 largest families that supply most of our species, only 4 (Poaceae, Asteraceae, Fabaceae and Liliaceae) together with one medium-sized family (Cyperaceae) supply over 50% of our indigenous weed species. Apart from Liliaceae (most of whose weed species are poisonous rather than invasive), these families appear to be strengthening their position relative to the remaining large families Mesembryanthemaceae, Iridaceae, Ericaceae and Asclepiadaceae.

If we ignore the vast areas of crop and wasteland covered by agrestal and ruderal weeds, and concentrate on the remaining areas of veld, we find that 50% of the weed species of natural pastures are supplied by the same five families that supplied most weeds of all kinds, plus one medium-sized family Malvaceae. A further change is that the weedy rôle of indigenous Poaceae is much lower in natural pastures than in adjacent crop and wastelands. This may well reflect vegetation changes shown in Fig. 1, where grass-dominated communities are giving way to karroid and arborescent communities in which most species are drawn from Asteraceae and Fabaceae.

Most indigenous families, even the weedy ones, contain more threatened species than weeds. The threatened species are more evenly distributed, 50% of them being supplied by 9 families: 6 large families (Iridaceae, Asteraceae, Liliaceae, Asclepiadaceae, Ericaceae and Fabaceae), together with 3 medium-sized families (Proteaceae, Orchidaceae and Santalaceae). The overall tendency seems to be for the large families to maintain or strengthen their positions relative to the smaller families.

As with indigenous weeds, the exotic weeds are concentrated in very few families. Practically 50% of all exotic weed species, and more than 50% of exotic species naturalized in the veld are provided by only 4 families: 3 large families — Poaceae, Asteraceae and Fabaceae, and one medium-sized family Solanaceae.

Three different patterns of success or failure within large and medium-sized families emerge from Table 1.

Pattern 1: large families containing many weeds and many threatened species, with the weedy side of the family being re-inforced by many exotics (Asteraceae, Poaceae and Fabaceae). Amaranthaceae, not shown in Table 1, exhibits a very similar pattern.

Pattern 2: large and medium-sized families containing few or no invasive indigenous or exotic weeds, but many threatened species (Iridaceae, Asclepiadaceae, Liliaceae, Mesembryanthemaceae, Ericaceae, Proteaceae, Orchidaceae and Santalaceae). Other families, not included in Table 1, that show this pattern, are: Rutaceae, Amaryllidaceae, Restionaceae, Bruniaceae, Crassulaceae, Campanulaceae, Polygalaceae, Rhamnaceae, Lobeliaceae, Portulacaceae and Zamiaceae.

Pattern 3: medium-sized families with very few indigenous weeds and threatened species, being supplemented by many exotic weed species (Solanaceae). Other families not included in Table 1, that show this pattern, are: Apiaceae and Polygonaceae (and many small families).

A fourth pattern, not represented here, is that of the 10 exotic families which between them supply 21 weed species, all of which are naturalized in the veld.

There are many variations of and intermediates between these patterns, but those shown here illustrate the main power shifts i.e. away from families showing pattern 2, (mostly centred in the

Cape) and towards those showing patterns 1, 3 and 4 (mostly centred in the more tropical parts of the country).

2.3 *Sub-family level*

An analysis of Fabaceae, one of the large families with many weeds as well as many threatened species, shows interesting differences at sub-family level (Table 2).

If the percentages in columns C, D and E are added (column G) it is seen that there is far less stress and expansion (9%) in the large sub-family Papilionoideae than in the other sub-families (Caesalpinioideae 45%, Mimosoideae 72%). In Papilionoideae the ratio of threatened species to weeds $\frac{C+E}{D}$ is also very different (0,7), compared to 3,8 in caesalpinioideae and 3,3 in Mimosoideae. There would appear to be a strong shift away from the more temperate, herbaceous Papilionoideae in favour of the other two more tropical and woody sub-families.

3 CONCLUSIONS

Many power shifts are taking place between indigenous species in the veld. Superficially, it seems as though a relatively few invasive species are displacing a larger number of threatened species, but evidence from Natal points to more species increasing than decreasing under conditions of over-utilization.

Amongst small families power shifts are almost as prevalent and important as at species level. Seventeen small families have over 20% indigenous weed species. Thirty small families have over 20% threatened species, and 21 small families have had their species numbers bolstered by more than 20% by exotic weeds.

A very few large and medium-sized families contain over 50% of our weeds and our threatened species. It is mostly temperate (Cape) families that are under pressure relative to most tropical families. This trend is echoed at sub-family level within the Fabaceae.

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Weed flora of South Africa 3: more power shifts in the veld

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ABSTRACT

This paper deals with shifts towards plants with particular life cycles, growth forms, or from particular geographic areas.

Exotics probably have their greatest impact in the aquatic habitat where they almost equal in number of species (the ratio is 3:5) and out-perform the indigenous aquatic flora. In the streambank habitat exotic weed species, mostly trees, outnumber indigenous weed species by more than 3 to 1. They are completely replacing indigenous streambank communities in many places. An investigation of their effect on stream flow and water loss is urgently required.

The problems of the winter rainfall area are highlighted by the fact that it has 300% more indigenous species and 109% more weed species per unit area than the summer and all year rainfall areas. In the veld as a whole there is a significant and so far unremarked invasion by exotic annuals.

The major invasive weed groupings are herbs from Europe and Asia and trees from Australia but South America probably has the greatest potential to provide us with new and dangerous weeds. A comparison of the weed floras of the southern continents could contribute much to an understanding of our own weed flora.

RÉSUMÉ

LA FLORE DES PLANTES NUISIBLES D'AFRIQUE DU SUD 3: AUGMENTATION DE LEUR AGRESSIVITE DANS LE VELD

Ce document traite des changements floristiques affectant les plantes à cycles de vie, formes biologiques ou distributions particulières.

Les exotiques ont probablement le plus puissant impact dans l'habitat aquatique où elles sont presqu',égales en nombre d'espèces (le rapport est de 3:5) et où elles ont un meilleur développement que la flore aquatique indigène. Dans l'habitat des berges les espèces exotiques les plantes nuisibles, pour la plupart des arbres, sont plus nombreuses que les espèces indigènes de plantes nuisibles dans un rapport superieur à 3:1. Dans beaucoup d'endroits elles remplacent complètement les communautés indigènes des berges. Une investigation de leur effet sur le courant et sur la perte en eau est requise de toute urgence.

Les problèmes de la région à chutes de pluies hivernales sont mis en lumière par le fait qu'elle a 300 % en plus d'espèces indigènes et 109% en plus d'espéces de plantes nuisibles par unité de surface que les régions à pluies d'été ou celles à régime de pluies durant toute l'année. Dans le veld dans son ensemble, il y a une invasion significative et jusqu'à présent non remarquée d'annuelles exotiques.

Les groupes majeurs de plantes nuisibles envahissantes sont des herbes d'Europe et d'Asie et des arbres d'Australie, mais l'Amérique du Sud a probablement la plus grande potentialité de nous fournir de nouvelles et dangereuses plantes nuisibles. Une comparaison des flores de plantes nuisibles des continents du Sud pourrait contribuer beaucoup à une compréhension de notre prope flore de plantes nuisibles.

1 INTRODUCTION

If it is true to say that scientists need to be as international as the material on which they work, then weed scientists should be the wandering Jews (or Arabs) of the science world. Certainly, it is impossible to work on South African veld weeds without becoming acutely aware of what is indigenous and what exotic. This harping on what is one's own and what is not, may seem strange to botanists from Europe where wave after wave of invading peoples and thousands of years of cultivation have mixed and blended, leaving an international flora. But the kingdoms of the south, the floras of Africa, America and Australia have evolved in isolation from one another, and from the great temperate plant reservoir of the northern hemisphere. These floras have unique characteristics and it is only in the last few hundred years that they have been brought together here at the southern tip of Africa. When they meet, it does not take a botanist or a poet to see them as green armies doing battle — that is exactly what they are.

With the battle-lines so clearly drawn, with our own flora one of the richest and most vulnerable in the world (Oliver, 1978) and with a fighting chance to save it, there is some justification for our preoccupation.

This paper deals with various habitats in the veld and with shifts towards plants with particular life cycles, growth forms, or from particular geographic areas. The weeds referred to are all in the National Weed List (Balsinhas *et al*, 1982).

2 LIFE CYCLES

The 966 exotic and indigenous weeds of the veld have been classified according to life cycle (Table 1).

The great majority of our weeds of the veld (particularly the indigenous ones) are perennials. The lack of indigenous annual weeds may be a real

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TABLE 1.—Life cycles of indigenous and exotic weeds of the veld

Life cycle	Flora and natural pasture weed species					
	Indigenous		Exotic		Total	
Annual	38	8%	152	32%	190	20%
Biennial/uncertain	17	3%	24	5%	41	4%
Perennial	430	89%	303	63%	733	76%
Total	485	100%	481	100%	966	100%

phenomenon or may reflect unintentional selectivity on our part i.e. that small annual indigenous species tend to be overlooked or are not considered important enough to be called weeds. Be this as it may, a significant invasion of the veld by exotic annuals is taking place. This invasion has gone almost unremarked and the roll of this new component in our veld needs to be investigated. It seems to be linked to bush encroachment, with exotic annuals colonizing the areas beneath invading trees.

3 HABITAT AND GROWTH FORM

The 1 003 exotic and indigenous species that are weeds in the veld and in water bodies have been classified according to habitat and growth form (Table 2). A number of them occur in several habitats, giving a total of 1 334 species for all habitats.

3.1 *Aquatic habitats*

The scarcity of water is the greatest limiting factor in the development of vast areas of South Africa. It is so valuable and large water-bodies suitable for recreation are so few that almost all plants growing in water are somewhere regarded as weeds. The 25 indigenous water weed species listed constitute almost our total indigenous aquatic vascular plant flora. They are mostly rooted species adapted to running water or to shallow waters of vleis and pans.

In terms of their percentage contribution to the flora of the habitat exotics probably have their greatest impact in the aquatic habitat, where there are almost as many exotic as indigenous species (the ratio is 3:5). However they do not always compete directly with indigenous species, and few indigenous aquatic species are endangered. This is because most of the exotics flourish best in standing and deep water situations, including man-made dams and canals.

3.2 *Streambank habitats*

The next greatest area of impact of exotics is probably the streambank-habitat, where exotic weed species outnumber their indigenous counterparts by more than 3 to 1 (Table 2). Most of these exotic invaders are woody trees and shrubs — growth

TABLE 2.—Growth forms of exotic and indigenous weeds in veld and water

Habitat	Growth forms	Number and %* of weed species					
		A Indigenous		B Exotic		C Total	
Aquatic	Hemi-crypt and floating	25	100%	15	100%	40	3%
Streambank	Trees & shrubs	8	27%	47	47%		
	Dwarf-shrubs & climbers	4	13%	10	10%		
	Hemi-cryptophytes	18	60%	44	43%		
	Streambank total	30	100%	101	100%	130	10%
Terrestrial Winter Rainfall	Trees & shrubs	30	23%	37	34%		
	Dwarf-shrubs & climbers	27	21%	4	4%		
	Hemi-cryptophytes	73	56%	68	62%		
	Terrest. W/R total	130	100%	109	100%	239	18%
[illegible]	Trees & shrubs	127	27%	145	31%		
	Dwarf-shrubs & climbers	77	17%	21	5%		
	Hemi-cryptophytes	261	56%	294	64%		
	Terr. All & S/R total	465	100%	460	100%	925	69%
		649		685		1334	100%

[illegible] habitat; in column C 100% = total species in all habitats.

forms that have a maximal effect on their neighbours, on lower strata and the habitat as a whole. Indigenous streambank communities are being completely replaced in some parts (Wells *et al.*, 1980) and there is an urgent need to establish what effect the new exotic communities are having on water loss and water flow.

The aquatic and streambank habitats occupy only about 1% of the area of the country but they are key areas where weeds have a high impact.

3.3 *Terrestrial habitats*

The terrestrial habitats that occupy 99% of the country are split as follows:

— the winter rainfall area covers about 11%, houses about 30% of our indigenous species, and about 18% of our weed species (both indigenous and exotic)

— the summer and all year rainfall area covers about 88% of the country, houses about 60% of our indigenous species and about 69% of our weed species.

The winter rainfall area has about 109% more weed species and 300% more indigenous species of all kinds per unit area than has the summer and all year rainfall area. If one realizes that most of the winter rainfall area has been drastically changed as a result of agriculture and urbanization etc., and that the rich Cape flora is concentrated in relic patches totalling 1,8 million ha (Hall *et al.*, 1980); that over 90% of these species are endemic (Oliver, 1977); and that they include the highest concentration of threatened species in the country, then the flora weed problem of the area is put into frightening perspective.

Terrestrial weeds are very evenly divided between exotic and indigenous species in both the winter and summer rainfall areas. The ratio of different growth forms also varies little with a lower percentage of dwarf shrubs and climbers and a higher percentage of trees and shrubs amongst the exotics. It is the exotic trees, particularly *Hakea, Acacia* and *Pinus* species, that have wrecked havoc in the Cape fynbos where a natural tree layer is lacking (Oliver, 1977; Hall *et al.*, 1980).

4 REGION OF ORIGIN

The region of origin of the 481 naturalized exotic weeds (flora weeds) and of the 16 exotic water weeds is shown in Table 3. A number of them occur in several habitats, giving a total of 685 species for all habitats.

Europe and Asia supply the largest number of flora weeds (40% of the total for all habitats). Of these 73% are hemi-cryptophytes or floating species and the region supplies 47% of all our flora weeds in this growth form category.

South America is the second largest contributor of flora weeds overall. Its species are well represented in all habitat and growth form categories and it contributes by far the most (60%) of the climbing and dwarf-shrub species, as well as the most water weeds.

Africa (and other) supplies mainly hemi-cryptophytes and water weeds of the summer rainfall area.

Australasia supplies only 11% of our flora weed species but of these a remarkably high proportion

TABLE 3.—Regions of origin of flora weeds of various growth forms and habitats

		Number and % of flora weed species									
		Region of origin									
Habitat	Growth Forms	Europe & Asia		Australasia		South America		Central & N.Am.		Africa & Other	
Aquatic	Hemi-cryptophytes & floating	3	20%	0	0%	6	40%	1	7%	5	33%
Streambank	Trees & shrubs	13	27%	13	27%	12	26%	5	11%	4	9%
	Dwarf-shrubs & climbers	1	10%	0	0%	9	90%	0	0%	0	0%
	Hemi-cryptophytes	21	50%	1	3%	6	14%	6	14%	10	19%
	Streambank total	35	34%	14	15%	27	28%	11	11%	14	12%
Terrestrial Winter Rainfall	Trees & shrubs	9	24%	22	59%	5	14%	1	3%	0	0%
	Dwarf-shrubs & climbers	1	25%	1	25%	2	50%	0	0%	0	0%
	Hemi-cryptophytes	43	63%	2	3%	9	13%	3	4%	11	16%
	Terrest. W/R total	53	49%	25	23%	16	15%	4	4%	11	10%
Terrestrial Summer & All Year Rainfall	Trees & shrubs	46	32%	26	18%	41	28%	21	14%	11	8%
	Dwarf shrubs & climbers	4	19%	2	9%	10	48%	0	0%	5	24%
	Hemi-cryptophytes	132	45%	8	3%	61	21%	34	11%	59	20%
	Terrest. All & S/R total	182	40%	36	8%	112	24%	55	12%	75	16%
Total all habitats:	685 (100%)*	273	40%	75	11%	161	24%	71	10%	105	15%

* For total flora weeds = 100% in each growth form category see Column B of Table 2.

(81%) are trees or shrubs. They are particularly important in the winter rainfall area but many of the species are invasive in all three non-aquatic habitats.

Central and North America is the least well represented region supplying mainly hemicrytophytes of the summer rainfall area.

At present it is not easy to know to what extent these patterns reflect the aggressive potentials of the other floras now interacting with our own. We have already suffered from the great influx of herbs from Europe and Asia, and of woody species from Australia. Our impression is that the greatest potential for future weed invasion is South America which has many hardy grasses like the Stipas, shrubs like *Larrea* and trees like *Prosopis* that have yet to penetrate to South Africa.

A comparison of the weed floras of the southern continents could contribute much to an understanding of our own weed flora and the hazards that await us in the form of new introductions.

5 CONCLUSIONS

Exotics probably have their greatest impact in the aquatic habitat where they almost equal in number of species (the ratio is 3:5) and out-perform the indigenous aquatic flora. In the streambank habitat exotic weed species, mostly trees, outnumber indigenous weed species by more than 3 to 1. They are completely replacing indigenous streambank communities in many places. An investigation of their effect on stream flow and water loss is urgently required.

The problems of the winter rainfall area are highlighted by the fact that it has 300% more indigenous species and 109% more weed species per unit area than the summer and all year rainfall areas. In the veld as a whole there is a significant and so far unremarked invasion by exotic annuals.

The major invasive weed groupings are herbs from Europe and Asia and trees from Australia but South America probably has the greatest potential to provide us with new and dangerous weeds. A comparison of the weed flora of the southern continents could contribute much to an understanding of our own weed flora.

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The weeds of abandoned cotton fields in Mozambique

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ABSTRACT

Based on a botanical survey of Chibuto, Chemba, Namapa, Nampula and Mutuali, a table of 120 of the most common weeds of cotton and fallow fields in Mozambique is presented. After considering the factors which affect the flora of these zones, the successional weed vegetation is described and the principal species are enumerated. Finally, the dangers of infestation (shrubby weeds in alluvial zones) and the utilization of the weed flora in other zones of the country are described.

RÉSUMÉ

LES MAUVAISES HERBES DES CHAMPS DE COTON ABANDONNÉS AU MOZAMBIQUE

Basé sur une prospection botanique des zones de Chibuto, Chemba, Namapa, Nampula et Mutuali, un tableau de 120 mauvaises herbes parmi les plus communes trouvées dans les champs de coton et les jachères au Mozambique, est présenté. Après quelques considérations sur les facteurs qui conditionnent la flore de ces zones, les aspects de la succession de la végétation des mauvaises herbes sont décrit et les principales espèces sont énumérées. Il est fait mention des dangers d'infestation (mauvaises herbes arbustives dans les zones d'alluvions) et de l'utilisation de la flore des mauvaises herbes dans d'autres zones du pays.

PLANTAS INFESTANTES DOS CAMPOS DE ALGODAO DE MOCAMBIQUE

Baseado em reconhecimentos botanicos a zonas do Chibuto, Chemba, Namapa, Nampula e Mutuali, o autor apresenta um quadro com 120 das mais comuns infestantes de pousios e campos de algodão de Mocambique. Faz depois consideraçoes acerca dos factores que condicionam a flora dessas zonas, descreve aspectos da sua sucessao e enumera os seus principais componentes; nas conclusoes refere-se aos perigos que podem advir da infestacao arbustiva nas zonas aluvionares e á utilidade da flora infestante em outras zonas do paìs.

OBSERVATIONS

The cultivation of cotton has had an important influence on economic development in the central and northern regions of Mozambique. The control of weeds in cotton fields in these regions has been a major problem for many years. Enforcement of control measures was responsible for socio/political trouble during the late 1940's and early 1950's.

In 1960 a survey was made of the weed vegetation of cotton and fallow fields (Lemos, 1961; Balsinhas, 1962). In this survey a large number of herbarium specimens was collected, and duplicates were sent to the herbaria COI, LISC, KEW, SRGH and PRE. Field notes including common and local names were recorded.

The present author then published the first check list of plants growing in cotton and fallow fields in Mozambique (Balsinhas, 1963). Research work and experimentation on herbicides was initiated in the same year (Almeida, 1970).

However, this is a vast subject and as Mozambique is traditionally an agricultural country it is essential that knowledge of the weed flora is improved. This is the motive for a further contribution to the subject using the existing information in the National Herbarium, Pretoria.

The notes on geographical distribution in Table 1 were compiled from the Flora Zambesiaca, Flora Tropical East Africa and Flora West Tropical Africa.

Analysis of the distribution of the species in the study areas (see Table 1) shows a difference in botanical composition indicating two distinct weed floras on distinct ecological sites. Weeds marked with an asterisk are abundant.

1. In the Chibuto and Chemba study areas on the flood plains of the Limpopo and Zambezi Rivers, there is a pantropical weed flora. Its distribution is influenced by edaphic factors as well as by the intensive cultivation of diverse food crops to supply the considerable human population. Here the major weeds are: *Abutilon grandiflorum, Acalypha segetalis**, *Amaranthus spinosus, Boerhavia diffusa**, *Brachiaria eruciformis**, *Cardiospermum halicacabum* var. *halicacabum, Chenopodium album, Cyperus rotundus**, *Hybanthus enneaspermus* var. *enneaspermus, Ipomoea sinensis* subsp. *blepharosepala**, *Leptochloa panicea**, *Portulaca oleracea, Zaleya pentandra**, etc. They are commonest in open places, in woodland, riversides, irrigated land, waste places and cultivated ground.

2. In the Nyassan sub-littoral and subplanaltic study areas, at Namapa and Mampula, and the south-central study area at Mutuali there is an abundant indigenous ruderal weed flora. Its composition and distribution is largely influenced by climatic factors and the cotton monoculture. The principal weeds are as follows: *Aspilia kotschyi* var. *kotschyi, Aspilia schimperi, Chrysanthellum americanum, Digitaria milanjensis, Digitaria setivalva**, *Eragrostis cylindriflora**, *Indigofera colutea* var.

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*colutea, Indigofera demissa, Mucuna coriacea**, *Oldenlandia caespitosa* var. *subpedunculata, Pennisetum polystachion, Rhynchelytrum repens**, *Sonchus bipontinii, Tricliceras longepedunculata* var. *eratense, Tridax procumbens**, *Vernonia ambigua,* etc. They occur in open woodland, grasslands, often in fallow fields or on old cultivation sites.

The weed flora of fields consists mainly of annual or herbaceous perennial plants. Manual weed control before the cotton is picked, eliminates most shrubby weeds. These become a problem in fallow fields only three or four years after cultivation has ceased. The more important shrubby species are: *Acacia polyacantha* subsp. *campylacantha**, *Cassia petersiana, Commiphora edulis, Cryptolepis obtusa**, *Markhamia obtusifolia**, *Monotes africanus** and *Tabernaemontana elegans.*

The succession of the weed vegetation in fields left fallow or when cultivation has ceased for about three years or more, is as follows:

1. Chibuto. Grasslands of *Brachiaria eruciformis, Hyparrhenia rufa* var. *rufa, Hyperthelis dissoluta, Leptochloa panicea, Sorghum verticilliflorum,* etc., with *Abutilon grandiflorum, Cardiospermum halicacabum* var. *halicacabum, Hibiscus vitifolius* subsp. *vulgaris, Ipomoea sinensis* subsp. *blepharosepala, Oxalis semiloba* subsp. *semiloba,* etc., Thorny shrub invasion of *Acacia nilotica* subsp. *kraussiana,* and sometimes *Acacia tortilis* subsp. *heteracantha,* etc.

2. Chemba. Grasslands of *Dactyloctenium giganteum, Digitaria milanjiana, Hyparrhenia rufa* var. *rufa, Panicum maximum, Pseudobrachiaria deflexa, Urochloa mosambicensis,* etc., with *Abutilon grandiflorum, Aerva tomentosa, Hermannia kirkii, Hibiscus caesius.* Cucurbitaceae include: *Ctenolepis cerasiformis, Cucumis anguria* and *Momordica kirkii; Sesbania mosambicensis* var. *mosambicensis, Vernonia kirkii,* etc. There is not much shrubby infestation except colonies of *Commiphora edulis.*

3. Namapa. Grasslands of *Aristida adscensionis, Eragrostis cylindrica, Hyparrhenia dichroa, Hyparrhenia filipendula* var. *filipendula, Panicum maximum, Pennisetum polystachion, Rottboellia exaltata.* In poorly drained soils, *Urochloa mosambicensis,* occurs, with *Aspilia kotschyi* var. *kotschyi, Sonchus bipontinii, Crotalaria virgulata, Mucuna coriacea, Tricliceras longepedunculata* var. *eratense,* etc. Shrubby invaders are *Acacia polyacantha* subsp. *campylacantha, Markhamia obtusifolia, Cassia petersiana,* etc.

4. Nampula. Grasslands of *Digitaria perrottetii, Digitaria setivalva, Eragrostis aethiopica, Eragrostis cylindrica, Hyparrhenia filipendula* var. *filipendula, Hyperthelis dissoluta, Panicum maximum, Pennisetum polystachion, Rhynchelytrum repens,* etc., with *Acalypha ciliata, Aspilia kotschyi* var. *kotschyi, Crotalaria virgulata, Indigofera colutea* var. *colutea, Mucuna coriacea, Sonchus bipontinii.* Shrubby invaders are *Markhamia obtusifolia* and *Tabernaemontana elegans.*

5. Mutuali. Grasslands of *Aristida adscensionis, Digitaria ciliaris, Eragrostis aspera, Eragrostis cylindriflora, Hyparrhenia rufa* var. *rufa, Hyparrhenia filipendula* var. *filipendula, Hyparrhenia variabilis, Leptocarydion vulpiastrum, Pennisetum polystachion, Rhynchelytrum repens,* etc., *Aspilia kotschyi* var. *kotschyi, Bidens schimperi, Chrysanthellum americanum, Indigofera demissa, Ocimum canum, Oldenlandia caespitosa* var. *subpedunculata.* The only shrubby invader seen was *Monotes africanus.*

CONCLUSIONS

As shown in Table 1, *Tribulus terrestris* and *Vernonia glabra* occur in all the study areas. The former species is largely disseminated, as a weed, in tropical and temperate regions throughout the world and the second is widespread only in tropical Africa. *Boerhavia diffusa, Corchorus tridens, Ocimum canum* and *Striga asiatica* are common tropical weeds and occur in four of the zones. The weeds that occur in one, two or three zones only, are more restricted to the environmental conditions described in the text.

If the fields in the alluvial zones are left fallow too long or without crop rotation, there is a danger that thorny thickets will develop which will rarely succeed to open grassy savanna. Once thickets develop the recurrent use of chemical products, to keep large areas of land clear, is both difficult and expensive.

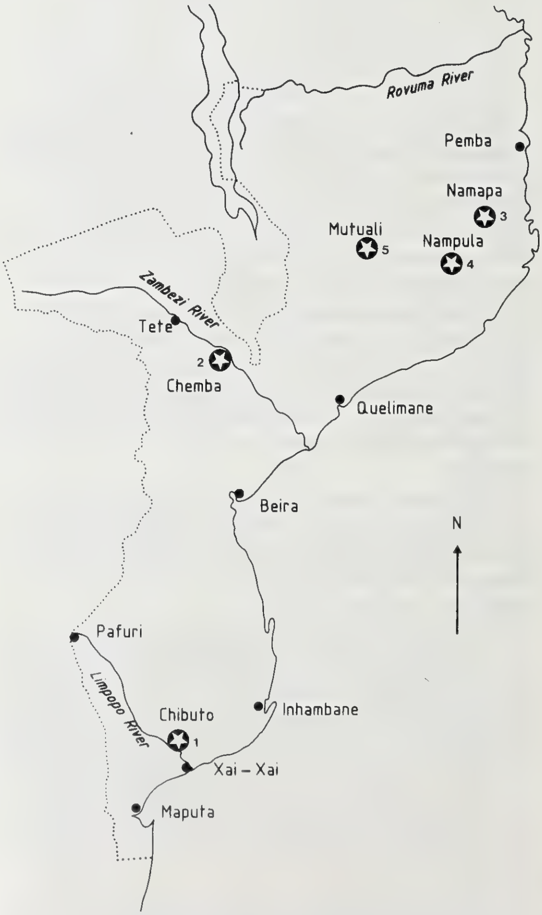

FIG. 1.—The positions of the areas studied in Mozambique.

TABLE 1. – The occurrence of weed species in five study areas in Mozambique (see Fig. 1)

Botanical name	Study areas*					Geographical distribution
	1	2	3	4	5	
Abutilon grandiflorum G. Don	+	+				Also in S. Tomé, Angola, Transvaal, Zululand and Madagascar
Acacia polyacantha Willd. subsp. *campylacantha* (Hochst. ex A. Rich.) Brenan			+			Widespread in tropical Africa from Gambia and Ethiopia (Eritrea) to Transvaal
Acalypha ciliata Forsk.				+		A widely spread weed in tropical Africa, Arabia and India
Acalypha indica L.		+				Through tropical Africa and Asia
Acalypha segetalis Muell. Arg.	+					Widespread in Tropica Africa
Acanthospermum hispidum DC.				+	+	Native of tropical America and now widely spread
Aerva tomentosa Forsk.		+				Extends from Mauritania through Africa to Arabia and India. Absent from Java
Amaranthus spinosus L.	+					Native of tropical America now widespread in warm countries
Argemone mexicana L.	+					Native of Central and tropical S. America. Widespread in all warm regions
Aristida adscensionis L.		+	+		+	Widely distributed in the warm and hot regions of the Old and New Worlds
Aspilia kotschyi (Schultz Bip.) Oliv. var. *kotschyi*			+	+	+	Extends from Sudan through East Africa to Angola. Also in Zanzibar
Bidens pilosa L.			+	+		Cosmopolitan weed
Bidens schimperi Sch. Bip. ex Walp.					+	From Ethiopia to Natal and westwards to Angola
Boerhaavia diffusa L.		+	+	+	+	Pantropical
Boerhaavia erecta L.		+			+	Widespread in the tropics of Old and New Worlds
Borreria scabra (Schum. & Thonn.) K. Schum.		+	+	+		Tropical Africa and Madagascar
Brachiaria eruciformis (J.E. Smith) Griseb. (B. isachne Stapf)	+					Widespread in the warmer parts of America; also in tropical Africa and southern Africa
Cardiospermum halicacabum L. var. *halicacabum*	+					Tropics and subtropics of the World
Cassia mimosoides L.			+			Widespread in tropical Africa and Asia
Cassia petersiana Bolle			+			Widespread in eastern Africa, extending from Ethiopia and the Sudan Republic, southwards to Zimbabwe Mozambique and South Africa. Also in Madagascar
Celosia trigyna L.			+			Widespread in Africa. Also in Arabia and Madagascar
Chenopodium album L.	+					Widespread in the temperate and warm parts of Northern Hemisphere; S. America and Australia; in Africa (other than N.); recorded from Congo, Mozambique and S. Africa
Chrysanthellum americanum (L.) Vatke					+	A cosmopolitan tropical weed
Cleome gynandra L. (Gynandropsis gynandra (L.) Briq.)	+					Widely distributed in Africa, Madagascar, Mediterranean region, Asia, Polynesia and tropical America
Cleome monophylla L.				+	+	Widely distributed through Africa and Ceylon
Commelina benghalensis L.	+			+		A common weed through the tropical and subtropical regions of Old World
Commelina undulata R. Br. (C. gerrardii C. B. Cl.)	+					North Australia, also found in Asia and Africa
Commiphora edulis (Klotzsch) Engl.		+				Botswana, Zambia, Zimbabwe and Malawi; also Transvaal and Tanzania
Corchorus tridens L.		+	+	+	+	Widespread in the tropics and subtropics of Old World
Corchorus trilocularis L.			+	+		Widespread as annual weed in Africa and Asia
Crotalaria virgulata Klotzsch		+	+	+		Tanzania, Mozambique, Malawi, Zimbabwe, Botswana and South Africa
Cryptolepis obtusa N.E. Br.				+		Tanzania, Mozambique, Zimbabwe and South Africa
Ctenolepis cerasiformis (Stocks) Hook. f. (Blastania cerasiformis (Stocks) A. Meeuse)		+				Old World tropics from Mauritania and Senegal east to India and in East Africa south to Transvaal
Cucumis anguria L.		+				Tropics of Africa, Australia and New World
Cyperus amabilis Vahl			+			Pantropical and subtropical
Cyperus rotundus L.	+					Pantropical and subtropical
Cyperus sphacelatus Rottb. var. *tenuior* C.B.Cl.				+		Throughout tropical Africa, Madagascar, Malaysia and N. Australia
Dactyloctenium aegyptium (L.) Willd.			+	+		Throughout the Old World tropics; introduced into America
Dactyloctenium giganteum Fisher & Schweick.		+				Tanzania, Zambia, Zimbabwe, Botswana, S.W. Africa and South Africa
Digitaria ciliaris (Retz.) Koel. (D. adscendens Henr.)				+	+	Throughout the tropics
Digitaria milanjiana (Rendle) Stapf		+				Congo, Angola, Zambia, Zimbabwe, Tanzania, Kenya, Malawi and South Africa; also in Madagascar
Digitaria perrottetii (Kunth) Stapf				+		Tropical Africa and Madagascar
Digitaria setivalva Stent				+		Uganda, Tanzania, Zambia, Zimbabwe, Botswana, S.W. Africa and South Africa
Eleusine coracana (L.) Gaertn.					+	Tropical Africa; also in East Africa from Ethiopia to Natal
Eleusine indica (L.) Gaertn.				+		Throughout the tropics
Eragrostis aethiopica Chiov.				+		Tropical Africa and South Africa
Eragrostia aspera (Jacq.) Nees		+		+	+	In tropical and South Africa, extending throughout Egypt and Arabia to India
Eragrostis cilianensis (All.) Lutati		+	+			Widely spread throughout tropics and warm temperate regions
Eragrostis ciliaris (L.) R. Br.			+	+	+	Throughout the tropics
Eragrostis cylindriflora Hochst. (E. horizontalis Peter)			+	+	+	Tropical and South Africa
Euphorbia hirta L.			+	+	+	Widespread in tropical and subtropical countries
Fimbristylis hispida (Vahl) Kunth (F. exilis Kunth)					+	Widespread in tropical and S.W. Africa
Gisekia pharnaceoides L. var. *pharnaceoides*	+			+		Widespread from Tropical Africa, South Africa and Mascarene Is. to India and Ceylon
Gisekia africana (Lour.) Kuntze		+				Widespread from tropical and Southern Africa to Asia
Hackelochloa granularis (L.) Kunze		+				Throughout the tropics
Hermannia kirkii Mast.		+				Botswana, Zimbabwe, S.W. Africa, Angola and South Africa (Transvaal); also in Kenya and Tanzania
Hewitia sublobata (L.f.) O. Ktze		+				Throughout tropical Africa, Asia, Malaysia and Polynesia, also in Jamaica as an escape
Hibiscus caesius Garcke		+				Tropical and subtropical regions of the Old World
Hibiscus sidiformis Baill.		+				Widespread in tropical and South Africa and in Madagascar
Hibiscus surattensis L.				+		Widespread in the tropics of the Old World
Hibiscus vitifolius L. subsp. *vulgaris* Brenan & Exell	+	+	+			Widespread in tropical and subtropical regions of the Old World
Hybanthus enneaspermus (L.) F. Muell. var. *enneaspermus*	+					From Senegal and the Sudan to Angola, Botswana, Transvaal and Natal; also in Madagascar, the Comoro Islands, Socotra, Arabia, tropical Asia from Ceylon to Haman, Malaysia and Australia
Hyparrhenia dichroa (Steud.) Stapf				+		Southern Africa from Zambia to Natal, and also in Sudan and Ethiopia
Hyparrhenia filipendula (Hochst.) Stapf var. *filipendula*	+		+	+	+	Throughout tropical Africa, and in Asia from Ceylon to Australia
Hyparrhenia rufa (Nees) Stapf var. *rufa*	+	+			+	Throughout tropical Africa, and also in tropical America. Introduced into most other tropical countries
Hyparrhenia variabilis Stapf					+	Eastern Africa from Ethiopia to the Transvaal
Hyperthelia dissoluta (Nees ex Steud.) W.D. Clayton	+			+		Now a cosmopolitan in the tropics and subtropics
Indigofera colutea (Burm. f.) Merr. var. *colutea*				+		Extending through Arabia, India and Indonesia to Australia and south to the Transvaal
Indigofera demissa Taub.					+	Congo (Katanga), Malawi, Zambia, Zimbabwe, E. Africa, S.W. Africa; also Madagascar
Ipomoea arachnosperma Welw.		+				Uganda, Kenya, Tanzania and throughout tropical Africa and India
Ipomoea coptica (L.) Roem. & Schult. var. *coptica*					+	Throughout tropical Africa, South Africa, Uganda, Kenya and Tanzania; tropical Asia and northern Australia
Ipomoea obscura (L.) Ker-Gawl. var. *obscura*	+					Throughout tropical Africa
Ipomoea pes-tigridis L. var. *pes-tigridis*		+	+			Extends to Sudan, Somaliland and S.E. tropical Africa; also in Mauritius and tropical Asia
Ipomoea sinensis (Desr.) Choisy subsp. *blepharosepala* (A. Rich.) Verdc.	+					In the tropics of Old World
Jacquemontia tamnifolia (L.) Griseb.				+		A native of tropical America, found there in all warmer parts, naturalized in tropical and South Africa, and the Mascarene Islands
Leptocarydion vulpiastrum (De Not.) Stapf		+			+	Tropical east Africa, central and southern Africa
Leptochloa panicea (Retz.) Ohwi	+					From tropical Asia now widely distributed in tropical Africa
Limeum sulcatum (Klotzsch) Hutch. var. *sulcatum*		+				Angola, South and S.W. Africa, Botswana and Zimbabwe
Markhamia obtusifolia (Bak.) Sprague			+	+		Congo, S.W. Africa, Zimbabwe and Botswana
Melhania forbesii Planch. ex Mast.	+	+				Zambia, Zimbabwe, South Africa (Transvaal), S.W. Africa and Angola
Mollugo nudicaulis Lam.		+	+			Pantropical
Momordica kirkii (Hook. f.) C. Jeffrey (Raphanocarpus kirkii Hook. f.)		+				S.W. Africa, Zambia, Zimbabwe, Malawi, Tanzania
Mucuna coriacea Bak. subsp. *coriacea*			+	+		Tanzania, Mozambique, Malawi and Zambia
Monotes africanus A. DC.					+	Angola, Tanzania, Malawi and Congo
Ocimum canum Sims	+	+	+		+	Africa, Asia and tropical America
Oldenlandia caespitosa Hiern var. *subpedunculata* (Kuntze) Brem.			+		+	Africa tropical and subtropical; Malgasciam and Syriam
Oxalis semiloba Sond. subsp. *semiloba*	+					Ethiopia, Kenya, Congo, Tanzania, Angola, Botswana, Zimbabwe, Zambia, Malawi and South Africa
Panicum maximum Jacq.		+	+	+		Throughout the tropics
Pennisetum polystachion (L.) Schult.			+	+	+	Throughout the tropics
Phyllanthus pentandrus Schumach. & Thonn.	+					Widespread in tropical Africa
Portulaca oleracea L.	+					A cosmopolitan weed of temperate and tropical regions
Portulaca quadrifida L.		+		+		Cosmopolitan as a weed in the tropics and subtropics
Pseudobrachiaria deflexa (Schumach.) Launert (Brachiaria deflexa (Schumach.) Hubb. ex Robyns)		+	+			Throughout tropical Africa, extending in to Arabia, Madagascar and South Africa
Pycreus pelophyllus (Ridl.) C.B. Cl.					+	Throughout tropical Africa and Madagascar
Rhynchelytrum repens (Willd.) Hubb.			+	+	+	Throughout tropical Africa and introduced to most other tropical countries
Ricinus communis L.	+					Generally believed to be native to Africa and India. Widespread in the tropics
Rottboellia exaltata L. f.		+	+			Throughout the Old World tropics and in the West Indies
Sesbania mossambicensis Klotzsch subsp. *mossambicensis*		+				Mozambique and Zimbabwe
Sida acuta Burm. f.				+		Widespread in the tropics and extending into S.W. Africa, Transvaal and Natal
Solanum panduraeforme E. Mey.			+			Widespread in tropical Africa
Solanum renschii Vatke		+				Tropical Africa
Sonchus bipontinii Aschers.			+	+		Uganda, Kenya, Tanzania; also in Ethiopia, Sudan, Rwanda and the Congo
Sonchus oleraceus L.	+					A native of Eurasia and N. Africa, now more or less cosmopolitan as a weed
Sorghum verticilliflorum (Steud.) Stapf	+					East tropical and southern Africa; Asia, Australia and W. Indies
Striga asiatica (L.) O. Ktze (S. lutea Lour.)		+	+	+	+	Widespread in tropical Africa and Asia, South Africa and the Mascarenes
Tabernaemontana elegans Stapf				+		Tanzania, Zimbabwe and South Africa
Tribulus terrestris L.	+	+	+	+	+	In tropical and temperate regions throughout the world
Trichodesma zeylanicum (L.) R. Br.			+	+	+	Distributed through India, Malaya, Australia and Africa
Tricliceras longepedunculatum (Mast.) R. Fernades var. *eratense* R. Fernandes			+			Known only from Mozambique. Endemic
Tridax procumbens L.			+	+	+	A native of central America, now widespread in tropical Africa, Madagascar, Asia and Australia. Also in South Africa
Triumfetta rhomboidea Jacq.			+			Known throughout the tropics and subtropics
Urochloa mosambicensis (Hack.) Dandy	+	+	+			Subtropical and southern Africa; Burma
Vernonia ambigua Kotschy & Perr.			+			Extending through the drier parts of tropical Africa to Sudan and Angola
Vernonia cinerea (L.) Less.	+		+	+		Widespread in tropical countries
Vernonia fastigiata Oliv. & Hiern	+				+	Tropical Africa
Vernonia glabra (Steetz) Vatke	+	+	+	+	+	Widespread in tropical Africa
Vernonia kirkii Oliv. & Hiern		+				Zambia, Zimbabwe and Mozambique
Vigna sp. (Balsinhas & Macuacua 543, at PRE)		+				–
Waltheria indica L.				+		Widely distributed through tropics and subtropics
Zaleya pentandra (L.) Jeffrey	+	+				Throughout tropical Africa from Transvaal to Egypt and Senegal; also in Arabia, Palestine and in Madagascar

* Study areas: 1, Chibuto; 2, Chemba; 3, Namapa; 4, Nampula; 5, Mutuali

In the sub-planaltic zones the succession on fallow and abandoned fields is towards a type of grassland with woody elements. In the first two years a thick, close sward is formed which, with correct management, can be useful for other agricultural activities such as grazing for cattle.

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The control of silky hakea in South Africa

S. R. FUGLER*

ABSTRACT

The introduction of *Hakea sericea* Schrad. from Australia to South Africa and the weed problems it presents today are described. The three methods of control currently used to combat this menace (mechanical, biological and chemical) are described and the integration of mechanical and biological control is advocated.

RÉSUMÉ

LA LUTTE CONTRE L'HAKEA SOYEUX EN AFRIQUE DU SUD

L'introduction de l'Hakea sericea *Schrad. d'Australie en Afrique du Sud et le problème de nuisance qu'il présente aujourd'hui, sont décrits. Les trois méthodes de lutte couramment utilisées pour combattre cette menace (mécanique, biologique et chimique) sont décrites et l'intégration des moyens de lutte mécanique et biologique est préconisée.*

INTRODUCTION

The genus *Hakea* belongs to the subfamily Grevilleoideae in the family Proteaceae. The Proteaceae are well represented in both Australia and South Africa, although the genus *Hakea* does not occur naturally in South Africa. *Hakea sericea* Schrad., commonly known as silky hakea (Stirton, 1978), is thought to have been introduced to South Africa in 1833 by the Baron C.T.H. von Ludwig (Annecke & Neser, 1977). The species *H. sericea* has many forms in Australia (Neser, 1968) and the form introduced into South Africa is thought to have originated from the Sydney area (Annecke & Neser 1977). The environment in the Sydney area is sufficiently similar to the south-western Cape to enable *H. sericea*, a plant introduced without its controlling agents (Neser, 1968), to grow vigorously. It seems that all *Hakea* species that have become pests (Fugler, 1979), were popular as hedging plants, although they also had other uses (Stirton, 1978). Phillips (1938) records that *H. sericea* became such a problem in the Knysna area that the local Farmers Association requested that the plant be proclaimed a noxious weed. This was done in terms of proclamations 161/1938 and 171/1940 of the Weeds Act, No. 42 of 1937. A literature review on *H. sericea* has been made by Fugler (1979).

PROBLEMS ASSOCIATED WITH SILKY HAKEA

Conservation problems

Silky hakea has colonized much of the mountainous area of the south-western and southern Cape. The natural vegetation of these areas is fynbos, a unique and threatened vegetation type (Taylor, 1978). The general distribution of *H. sericea* is shown in Fig. 1. The extent of infestation is not reliably known, but available figures are given in Table 1 (Fenn, 1980, Directorate of Forestry records, unpublished). *H. sericea* is able to establish abundant populations in a few generations. Such populations almost eliminate the natural communities under them. Although no accurate information as to the precise nature of these effects is available, such invasion is certainly detrimental to the natural fynbos vegetation. Kruger (1977a) states 'it is clear that weed populations in the natural veld are totally incompatible with the conservation of the Cape fynbos'.

Effect on catchment water supplies

The effects of afforestation on catchment streamflow are well documented in South Africa (Banks & Kromhout, 1963; Wicht, 1967 and Malherbe, 1968). The information shows that conversion from low plant communities such as grass- or shrublands to forest almost invariably results in a decline in streamflow (Kruger, 1977a). Since *H. sericea* is a small tree, dense infestations could be expected to decrease streamflow. A hydrological project conducted by the Directorate of Forestry is seeking to answer this question.

Effect on fire hazard

The fynbos vegetation of the Cape is susceptible to fires which may be difficult to contain (Kruger, 1977a). Experience has shown that *H. sericea* changes the nature of the fire control problem. Since *H. sericea* stands contain a greater proportion of coarse flammable fuels than the native fynbos species, the potential for blow-up fires, especially under severe weather conditions, is increased where *H. sericea* is dominant (Kruger, 1977b).

CONTROL MEASURES

Mechanical control

Early attempts at the manual control of *H. sericea* were not always successful. Common mistakes included cutting the plant above the lowest green leaves, thus enabling the plant to survive; failing to burn the area before seedlings produced fruit; lack of follow-up to remove surviving plants after burning; and a lack of co-ordination between parties involved in clearance operations. In 1976 the Department of Forestry (now the Directorate of

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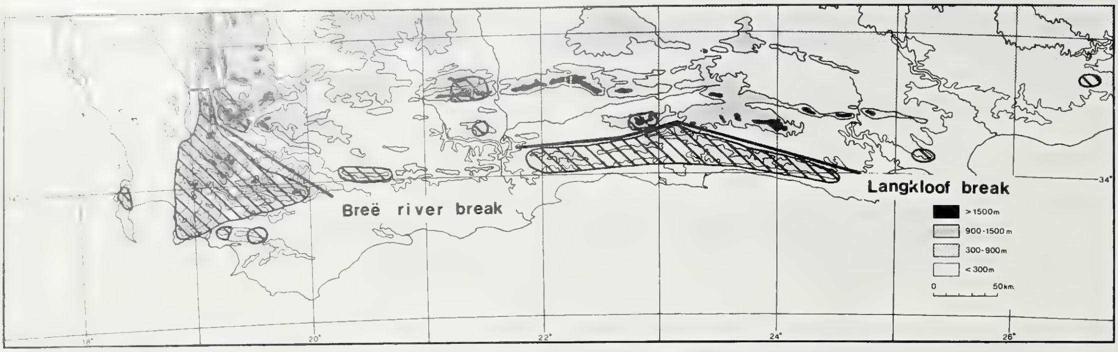

FIG. 1.—The distribution of *Hakea sericea* in the Cape Province, South Africa.

TABLE 1.— Known extent of *Hakea sericea* infestation in the Cape Province

Degree of Infestation	Area infested (ha)		
	Western Cape Forestry Region	Southern Cape Forestry Region	Tsitsikamma Forestry Region
Dense	8 600	15 220	7 609
Medium	184 000	16 270	15 559
Sparse	192 000	38 930	11 851

* Dense = Stems less than 4 m apart

Medium = Stems more than 4 m apart, but individual plants always visible

Sparse = Individual plants present but not always visible.

Forestry in the Department of Environment Affairs) started a mechanical eradication programme (Fenn, 1980).

The mountainous fynbos areas under the control of the Directorate are divided into management units termed compartments. These range from 100 ha to 1 000 ha in size, depending upon the terrain and degree of infestation by alien vegetation. They are burnt on a 12-year cycle which enables the fire-adapted fynbos vegetation to regenerate (Van Wilgen, 1980). All *H. sericea* plants present in the compartment are cut down before burning. The distances that labour operates from Forest Stations sometimes necessitates the building of temporary huts in the mountains from which the crews operate for five-day stints. The felling of *H. sericea* is carried out using a combination of slashers, beanhooks, bowsaws, mechanical bush cutters and chainsaws (Le Roux, 1978).

The cut plants are left to lie for 12 to 18 months. During this period the fruit on dead plants opens and releases the winged seed. This has little chance of being blown any distance as the parent plant is no longer standing upright. Seeds germinate around the fallen parent plants, but before they produce fruit the compartment is burnt, destroying the seedlings. [illegible] years after the fire the area is searched and [illegible] ng *H. sericea* seedling found is pulled out. This task is called 'follow-up' and is considered to be the most arduous part of the control task (Le Roux, 1978).

Mechanical control is the most effective eradication method known at present. During the period 1976 to 1979 *H. sericea* was cleared from 13 376 ha in the western Cape Forestry Region (Fenn, 1980) and 17 267 ha had been cleared from the Southern Cape Forestry Region by the end of 1980 (H. Wilhelmij pers. comm., 1980). *H. sericea* infestations occurring on private land are a serious problem and the legal situation is at present under review. The Directorate hopes to clear the mountains of *H. sericea* in the next ten years but as the programme advances the amount of follow-up work will snowball.

Biological control

Biological control was initiated in 1962, when Webb was sent to Australia to investigate possible controlling agents (Annecke & Neser, 1977). Neser (1968) continued the work and noted that in areas of Australia where seed attacking insects were absent, *H. sericea* produced large numbers of fruit as did the plants in South Africa.

The destruction of large numbers of seeds in perennial plants is normally considered of little value for biological control. Neser reasoned that this did not apply to *H. sericea,* as its reproductive strategy is similar to that of annual or biennial weeds, because the fruits are retained on the plant and released in large numbers after its death. The only real difference between *H. sericea* and annual or biennial weeds is the time period between generations. The destruction of large amounts of *H. sericea* seed is therefore regarded as a useful control method (Neser, 1968).

No indigenous South African Proteaceae have similar fruits to *H. sericea* and seed-attacking insects show a high degree of specialization (Neser, 1968). For this reason, it was thought safer to release seed-attacking insects than insects that attack vegetative parts of the plant. Seed-attacking insects that have been released are the hakea fruit weevil, *Erytenna consputa* Pascoe (Annecke & Neser, 1977) and the hakea seed moth, *Carposina autologa* Meyrick (S. Neser pers. comm., 1977).

E. consputa is now well established at some 99 release sites in nearly all the infested mountain ranges between Cape Town and Grahamstown. More releases are planned with the emphasis on the southern Cape. At one of the release sites where the weevil damage is being measured, 58% of the 1980 fruit crop was destroyed by *E. consputa.* It is confidently expected that this will still increase substantially (R. Kluge pers. comm., 1981).

Progress with *C. autologa* has been slow since large numbers are required for establishment. Research on better breeding methods is continuing (S. Neser and R. Kluge pers. comm., 1980). Once established, however, *C. autologa* should complement *E. consputa* very well, by further reducing the seed store in the developed follicles on the trees.

More recently a less conservative, but still very safe, approach has been taken and some attention has been given to insects attacking the vegetative parts of plants. It is hoped that these insects will supplement the seed-attacking insects (R. Kluge pers. comm., 1980). A leaf-boring weevil, *Cydmaea binotata* Lea, was found to be specific to *H. sericea* and released in 1979. It is hoped that this insect will reduce the growth and competiveness of seedlings. Research on a weevil *(Dicomada rufa* Blackburn) that destroys flower buds has started and further work on a variety of insects is planned for 1981 and 1982 (S. Neser and R. Kluge pers. comm., 1980).

An endemic fungus identified as a *Collectotrichum* state of *Glomerella cingulata* (Stotem.) Spauld. and Schenk also attacks *H. sericea.* The disease occurs widely and is common in many *H. sericea* stands. Areas of *H. sericea* with more than 90% natural infection and many dead plants have been observed in both the southern and south-western Cape. The long-term effects of the disease on such populations have yet to be determined. The fungus is easily grown in culture and methods of encouraging the spread of the disease are also being investigated. Inoculation of *H. sericea* with the fungus has resulted in the development of symptoms of the disease, which causes cankers to develop on the stems and branches and may eventually girdle and kill them. Shoot tips may also become infected and die (M. J. Morris pers. comm., 1980).

Chemical Control

The development of herbicides is a costly and time-consuming process. Stricter regulations on the properties of herbicides has resulted in increasing the financial risk of herbicide development. Fewer companies are now committed to this form of research and they are producing fewer marketable herbicides per annum (Naylor, 1979). Thus the herbicides produced tend to have a broad spectrum effect, and there is little chance of a specialized *H. sericea* herbicide being produced.

Roundup (glyphosate) and Garlon (triclopyr) have been applied to *H. sericea.* The results from the glyphosate trials were disappointing. In a mature stand, not all individuals were killed and the stands could not be burned as originally planned. Garlon was found to achieve satisfactory control on plants 1–2 m tall. These herbicides are broad spectrum and expensive and therefore unsuitable (D.G.M. Donald pers. comm., 1980). Streamflow from the mountains is used for agriculture and as drinking water; introducing chemicals into the mountains would therefore be a dubious practice and should be avoided whenever possible.

CONCLUSIONS

It seems unlikely that any significant contribution to the control of *H. sericea* will be forthcoming from herbicides, largely because of their lack of specificity and cost.

Mechanical control as applied by the Directorate of Forestry has made great strides since 1976, and is at present the most effective way of removing the existing stands. Being a mechanized, labour intensive method, its feasibility is subject to increase in the cost of labour, equipment and fuel.

The biological control programme is starting to produce noteworthy results and indications are that *Erytenna consputa* will be causing a significant reduction in seed production in the near future. This will, it is hoped, have short-term benefits by reducing the need for follow-up work. In the longer term, however, together with *Carposina autologa,* it is forseen that *E. consputa* will prevent the build-up of seeds on isolated plants, or on plants in inaccessible places. This will reduce the aggressiveness of the weed.

Because of a lack of proper evaluation the contribution of the disease caused by *Collectotrichum* has been underestimated. Now that it is the subject of a research project, its significance is likely to be recognized and it will be possible to make more effective use of it in the control effort. It can be used in combination with mechanical control, where it has proved extremely effective in killing cut stumps that still have fruit on them. The pathogen could be applied by brushcutter blades or by hand brushes, thus ensuring that these fruits also release their seed before the area is burnt.

In order to ensure the build-up and survival of a viable population of controlling insects, small areas of *H. sericea* should be left untreated. As long as these 'reserves' are not burnt, seeds will remain on the adult plants, thus preventing their spread. A combination of mechanical control and subsequent follow-up by both human and insect agents shows good promise of bringing *H. sericea* under control.

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Threatened plants at the south-western corner of Africa

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ABSTRACT

An account is given of the extent of floristic and habitat destruction in the area currently and formerly covered by the Cape Floristic Kingdom. An evaluation is given of the proportions of habitat threats and other factors affecting a sample of critically rare species. It is shown that invasive plants introduced from other countries pose a major threat to critically rare species in the areas where natural vegetation has not been fully replaced by suppressive land-uses. The value of the Cape Flora as a genetic resource for purposes such as an expanding cut-flower export-industry is demonstrated and research needs in this field are outlined.

RÉSUMÉ

PLANTES MENACÉES DANS LE COIN SUD-OCCIDENTAL DE L'AFRIQUE

Un compte rendu de l'étendue de la destruction de la flore et de l'habitat dans la région actuellement et antérieurement couverte par l'Empire floristique du Cap, est donné. Une évaluation des proportions des menaces pour l'habitat ainsi que d'autres facteurs affectant un échantillon d'espèces critiquement rares est donnée. Il est montré que des plantes envahissantes introduites d'autres pays créent une menace grave pour les espèces critiquement rares dans les régions où la végétation naturelle n'a pas été complètement supprimée par l'exploitation du sol. La valeur de la flore du Cap en tant que ressource génétique pour des buts tels qu'une expansion de l'industrie d'exportation des fleurs coupées est démontrée et les besoins de rechereches dans ce domaine sont soulignés.

INTRODUCTION

The aim of this paper is to examine the methods of study, results and reactions to the unusually severe threatened-plant problem in the south-western Cape Province, South Africa. The setting for this problem is the belt of coastal mountains and flats carrying the peculiar protea, heath and restio flora, known, because of its richness in species and distinctness of taxa, as the Cape Floristic Kingdom. The Cape Kingdom is by far the smallest of the six into which the world's terrestrial vegetation is divided (Good, 1964; Takhtajan, 1969; Hall, 1978). Having about 6 000 species in natural areas formerly totalling 4,6 million hectares, it is the most species-rich major floristic region in the world (Hall, 1978). Excluding minor outliers, the Cape Kingdom's area passes from Vanrhynsdorp 250 km south to Cape Town, and thence 800 km eastwards to Grahamstown, in a sometimes patchy belt 40–150 km wide. Succulent karoo floras, grasslands and Afro-montane forests are distinct elements of the Palaeo-tropical Kingdom that penetrate the belt, but which are excluded from consideration in this paper owing to their different habitats, distribution patterns and less severe threatened-plant problems.

METHODS

A survey of threatened plants in the western Cape Province was started in 1974. A team of two graduate assistants searched herbarium records, literature and communications from specialists on various taxa, looking for candidate species for the threatened-plant list. The criteria for listing excluded taxonomically doubtfully distinct species, but included significantly different or 'important' infraspecific taxa. As the Cape Kingdom has been fairly well recorded in herbaria, the presence of few herbarium specimen-localities could be taken as a reasonable indicator of rarity. This, coupled with general knowledge of the intensity of replacement of natural habitats by other land-uses, gave what proved to be a fairly reliable list of candidates for field study.

The field-studies were planned from regional, monthly lists of taxa made from data compiled in dossiers on each species. Each species-dossier carries a photograph of a specimen or a copy of an illustration, a taxonomic description, and a list of localities and flowering-times. The A4-size card bearing these data can be put into a protective transparent folder for field use. Indexes and monthly lists of taxa for each ¼ × ¼ degree area were prepared with the aid of a computer-based data-bank (Hall, 1981). Data are collected at the sites of threatened-plant populations according to a schedule which covers geographical distribution, habitat features, population biology, threats to survival and recommendations for conservation (Hall *et al.*, 1980b). Reports of this kind have been completed for about 350 species, with others only partly complete pending further visits to field sites.

Where the survey has revealed locally high concentrations of threatened and critically rare plants, a regional report is drawn up bringing together the findings on all threatened species and habitats in the area, for use in planning sanctuaries and nature reserves.

The preliminary findings of this and other surveys were published as lists of threatened and rare taxa for Southern Africa (Hall *et al.*, 1980b). This snapshot view is being supplemented by a gazette carrying data on the changing survival-status and actions being taken on especially critical taxa in the Cape Kingdom. This gazette will be produced

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TABLE 1.—Estimated numbers of vascular plant species that are threatened, critically rare or recently extinct in the Cape Floristic Kingdom. The categories are those defined by the IUCN (Lucas & Synge, 1978)

IUCN category	Number of species
Recently extinct	36
Endangered, close to extinction	98
Vulnerable and declining	137
Critically rare	383
Indeterminate, in one of the above categories	279
Uncertain, probably in one of the above categories	688
Total	1 621

periodically from a computer data-bank where the information will be accumulated.

RESULTS

The current estimates of the numbers of threatened, critically rare and recently extinct vascular plants in the Cape Kingdom are given in Table 1. The former natural area of the Cape Kingdom, prior to partial replacement by agriculture and other land-uses, is estimated to be 4,6 million hectares. This is less than 2% of the area of Southern Africa (including South West Africa/Namibia and Botswana). It is remarkable that the Cape Kingdom has, in this small area, 68% of Southern Africa's plants in hazard (Hall *et al.*, in press).

The chief threats affecting these plants are shown in Table 2. By far the worst threat is the invasion of plant habitats by escaped alien species brought to the Cape mainly from Australia and Europe for binding drift-sands, hedges, timber, tannin production, firewood and stock-feed supplements. Although these thicket-forming alien plants remain useful in several of these ways, their indiscriminate introduction and natural spread into wild flora areas today gives widespread concern for the future of the Cape Floristic Kingdom (Shaughnessy, 1980; Hall & Boucher, 1977; Hall, 1979). The chief problems are that the introductions are well-adapted to the widespread nutrient-poor soils in the Cape Kingdom, are encouraged by periodic fires, and in the case of the especially dangerous Australian Acacias, have a massive production of long-lived seed which is not heavily damaged by insects as in the plants' land of origin (Milton & Hall, 1981). Most of the other threats are directly related to human population growth and the consequent need to expand areas of intensive land-usage. Plants in the Cape Kingdom quite often have rather localized distributions, some naturally as small as a few hectares. Quite minor expansions of land-uses may significantly damage or even destroy a species' only population. For example, a single quarry has destroyed the habitat of *Moraea loubseri,* making it extinct in the wild. Human population-growth in the south-western Cape remains rapid, having had a total increase by one-fifth in the 1971–1980 census decade. The region is an important source of agricultural produce for Southern Africa which has a total monthly population increase of about 60 000 persons, which lays yet further stress on local agricultural expansion.

TABLE 2.—The chief destructive habitat pressures affecting wild plants in the Cape Floristic Kingdom, and the percentage of a sample of 200 threatened, critically rare or extinct species affected in each case (from Hall *et al.*, 1980a)

Habitat pressure	% of sample affected
Invasion of habitat by alien plants	54
Ploughing and related agricultural activities	26
Urban and industrial expansion	24
Over-frequent fires in vegetation	20
Grazing and browsing by livestock	14
Wild flower-picking for pleasure or profit	7
Road construction	6
Trampling	6
Dam construction	4
Quarrying	3
Afforestation	2
Natural pathogens	1

These conditions lie in sharp contrast to Europe, where the flora appears to be more robust, perhaps from its post-glacial pioneer origins, and where plant distributions are seldom as miniature as those quite often found in the Cape. Furthermore, the combination of threats from population growth in Europe seems to be less: however, perhaps losses went unrecorded during such episodes as the deforestation for expansion of agricultural land in the Middle Ages.

Similar unrecorded depradations may have taken place in the south western Cape lowlands. There is archaeological evidence that by 2 000 years ago, pastoralists were herding sheep and burning vegetation in this area to promote fresh growth. When historical records began some 300 years ago, there were already several thousand Hottentots living on the Cape Flats.

Their impact upon the vegetation, especially any sensitive and local rarities, would have been considerable. Numbers of plants may have already become extinct in the lowlands and others may have become so rare that their later extinctions went unrecorded by the early plant-collectors. This may partly account for the fact that only some 40% of the Cape Kingdom's plants in hazard are from the lowlands (below 300 m) where the most widespread replacement of natural vegetation has taken place in historical times (Hall *et al.*, 1980a).

REACTIONS TO THE THREATENED-PLANT PROBLEM

The Cape Kingdom is recognized as a crisis zone for the loss of genetic diversity. This statement encompasses not only the plants that are being made extinct but also the many others that have had their variability reduced by the widespread losses of local populations (Hall *et al.*, 1980b).

A common but misleading belief is that a permanent solution can be sought by holding small samples of natural populations in horticulture. These small populations are genetically at risk, especially in the case of short generation time species such as annuals, which may, relatively rapidly, drift away from the original richly varied gene-pool, perhaps with deleterious inbreeding effects. This may be accentuated by the alien conditions of horticulture, in artificially fertilized and watered soils; also microclimates that due to spaced arrangements and weeding may be unfamiliar to plants used to crowded conditions in the wild; and, finally, an absence of pollinators and other associates which may be necessary for survival. Other hazards may be new opportunities for hybridization, perhaps taking place introgressively at a low but significant frequency and not previously experienced by the species in the wild; finally, there is the risk of catastrophic loss of the species by disease if all the plants are held in the same area. Failure of the horticultural option may also take place if interest in conserving the plant by growing it should become lessened by change of staff, loss of records or simple lack of concern. Long-term conservation should, in this light, clearly take place in wild habitats where there exist the pressures and amenities that had caused adaptations in the populations of the species in the past. The chief rôle of horticulture for threatened species should be to provide a temporary home for raising large numbers of individuals for use in restoring natural populations in the wild (Hall & Rycroft, 1979).

With the patchy nature of many of the Cape Kingdom's relics, wild populations of some species will need to be monitored and cared for on a semi-horticultural, management basis. Based on 1972 Landsat imagery and other observations, only 39% of the wild vegetation remains, much of it penetrated and diluted by invasive thickets of alien species (Hall, 1978). Costly restoration plans are already under way in mountain catchments to remove alien vegetation: in a single twelve-month period in 1980/1981 over 28 000 hectares of Australian Hakea were cleared in the south-western Cape alone (J. A. Fenn, pers. comm.). Buffer-zones will need to be created around restored areas to cushion them from external impacts: to this end, recent legislation allows alien plant clearing up to 5 km outside the catchment boundary. This good progress in offsetting the effects of insularization in mountain areas is at present only weakly reflected in the lowlands, although there are encouraging glimmerings of change. The lowlands are virtually all held in private ownership and a communication problem must be overcome before the threatened-plant crisis there can be solved.

It is relatively simple matter to communicate the need for action directly from a research unit to a receptive body such as a conservation or forestry authority: in fact this is a well-worn channel for a steady flow of scientific findings.

Communication to private, profit-orientated land-owners presents considerable difficulties, especially within the rather limited confinements of local and Provincial funding. There is barely any educational tradition to appeal to: school curricula have only recently included the conservation of flora in biology courses. There are virtually no adult-guidance programmes such as local interpretive centres. Only one small museum, at Hout Bay on the Cape Pensinsula, carries an adequately comprehensive exhibit on the threatened-plant crisis. Such guidance is also virtually absent in the few private and subsidized nature reserves in the lowlands. A little information is available on some of the more common species in illustrated books, dealing with parts of the lowlands. One may conclude from this that there is little reason to expect public pride, concern and interest in the lowland flora. With a few distinguished exceptions, this is true of most lowland landowners. Commercial activity, in utilizing the flora for the R3 million cut-flower export industry, is of value in conserving a limited number of more spectacular species, 65% of which are taken from the wild, mostly in the nearby mountains. For general picking of supporting foliage ('Cape Greens'), the industry may be hazardous for the less easily recognized threatened species. The cut-flower industry is a marginal activity over most of the lowlands, where good-quality soils are better suited to more profitable food-production. For many landowners, the conservation of the flora, even of threatened species, may have a hobby-like ring to it, a pastime or naturalist's activity entirely divorced from the practicalities of farmland management.

Conservation of threatened lowland plants should be preceded and accompanied by adult guidance on a large scale to reach most landowners. The methods should fall into the category known as environmental interpretation (Sharpe, 1976). These are defined as programmes which are given in a leisure setting, at the site of a natural phenomenon, and are 'neither education nor entertainment alone, but a subtle mixture of both.' The programmes require interpretive centres, self-guided trails through nature areas, conducted visits, short entertaining talks and supporting information channelled through pamphlets, books and the public media (Hall, 1983). The aim is to generate a strong tone of pride-of-place and personal involvement through local participation. Once started, the programmes are surprisingly efficient in generating an adequate ethic that allows and encourages conservation actions to go ahead: this has been shown particularly well in both the built and the natural environments in Europe. The effect is to guide people into a cultural appreciation of nature. More importantly, it can help show humanity's critical dependence on the intactness and proper functioning of the biosphere (Polunin, 1980).

CONCLUSIONS: POSSIBLE RELEVANCE ELSEWHERE IN SOUTHERN AFRICA

Hedberg (1979) has reviewed the possibilities and needs for conservation of plant species and vegetation in Africa. The main needs identified were basic taxonomic data and the practical application of theory by means of functional conservation bodies. Meeting the taxonomic needs lies squarely in the hands of botanists who provide the primary flora treatments. The provision of functional conservation bodies cannot be adequate without, in the first place, public support for funding for staff and equipment. This support must come from public interest otherwise the programmes may become, in a sense, artificial and, unless self-reinforcing, could eventually fail. Public interest is also needed if reserves for flora are to be made by subtraction from land in private ownership or publicly used commonage. Scientists and conservators owe the public an explanation for their wishes to set aside land as reserves and to undertake costly conservation programmes. The explanations should show in clear terms the benefits of having the reserves. The best ways of putting across these important ideas appear to be by the methods of environmental interpretation, which is likely to have a critically important future rôle in the conservation of the great plant life of Africa.

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The conservation of *Aloe polyphylla* endemic to Lesotho

S. TALUKDAR*

ABSTRACT

Aloe polyphylla Schonl. ex Pillans, the spiral aloe, has been declared a protected species in Lesotho since 1938, yet the plant has been declining in number. Since then changes have taken place, including accelerated road building programmes, which make the problem of conservation of the species in its natural habitat even more acute. Problems connected with this rare species are discussed. It is concluded that, whereas measures initiated show some success, much more needs to be done.

RÉSUMÉ

*LA PROTECTION DE L'*ALOE POLYPHYLLA *ENDÉMIQUE AU LESOTHO*

*L'*Aloe polyphylla *Schonl. ex Pillans, l'aloè spiralé, a été déclaré espèce protégée au Lesotho depuis 1938, et cependant la plante a continué à décliner en nombre. Depuis lors, des changements sont survenus, incluant des programmes de constructions routières accélérés qui rendent le problème de protection de l'espèce dans son habitat naturel de plus en plus aigu. Les problèmes inhérents à cette espèce rare sont discutés. En conclusion, bien que les mesures prises montrent un certain progrès, il reste encore beaucoup à faire.*

INTRODUCTION

Aloe polyphylla Schonl. ex Pillans, the spiral aloe, called lekhalakhare and lekhala-la-kharatsa in Sesotho, was first collected by F. H. Holland on Phurumela (Furumela) Mountain in November 1915. The material was sent to Schonland of the Albany Museum, Grahamstown, who drew up a description in January 1923 naming the plant *A. polyphylla,* but the description was never published. In 1934 Pillans published a description using Schonland's MS name and basing his description on Schonland's notes as well as photographs and material collected by Reynolds from Phurumela in September 1934.

The spiral aloe is unique to Lesotho and has not been found growing naturally outside Lesotho's borders. The plants are distinctive with five ranks of leaves that are coiled in either a left-handed or a right-handed spiral and have been much sought after by plant enthusiasts. The restricted distribution and the sale value of the spiral aloe have resulted in a serious depletion of the number of plants, causing its name to appear in the International Union for Conservation of Nature (IUCN) Plant Red Data Book (1978) as a vulnerable species. It is, moreover, included in Appendix 1 of the 1973 Convention on International Trade in Endangered Species of Wild Fauna and Flora.

The Government of Lesotho has in recent years given high priority to road building, with a number of road projects specifically aimed at providing improved communications in the remote mountain areas. The remote mountain areas are also the home of *A. polyphylla.* As the hitherto remote areas become accessible, the spiral aloe sites also come within easier reach, and are therefore rendered more vulnerable. The matter of protecting this very distinctive aloe of Lesotho is now an urgent one. Beverly (1978) estimated the spiral aloe population to be around 3 000 plants. The known distribution is shown in Fig. 2.

CONSERVATION PROBLEMS

Plants removed from their natural habitat are difficult to grow. Gardeners often kill them by overwatering or by not watering them at all. They grow slowly and their fruits frequently get damaged by insects. The seeds that survive do not germinate if conditions are not right and the seedlings may show frost sensitivity (Beverly, 1977). The problems of maintaining a spiral aloe population are not only those of law enforcement, but also a lack of knowledge of the plant's life cycle and ecology.

The problem of conservation of *A. polyphylla* is being tackled in three ways: by legislation, publicity and education, and by the raising of plants in an authorised nursery in Maseru. These programmes have not been as effective as they might be because of a lack of enough trained people to carry them out. Enforcement also needs its own budgetary provision.

LEGISLATION

Aloe polyphylla was declared a protected plant by a Proclamation issued by the Resident Commissioner of Basutoland on the 20th September 1938, prohibiting its removal, export, sale or destruction. This Proclamation was repealed and replaced by the Historical Monuments, Relics, Fauna and Flora Act, Act 41 of 1967 of Lesotho Government.

Act 41 of 1967 made provision for a Commission for Preservation of Natural and Historical Monuments, Relics and Antiques and the Protection of Fauna and Flora (Section 3). This commission known as the Protection and Preservation Commission (PPC) was given the tasks, 'subject to the provisions of this Act, generally of performing all such acts as are necessary for or incidental to the

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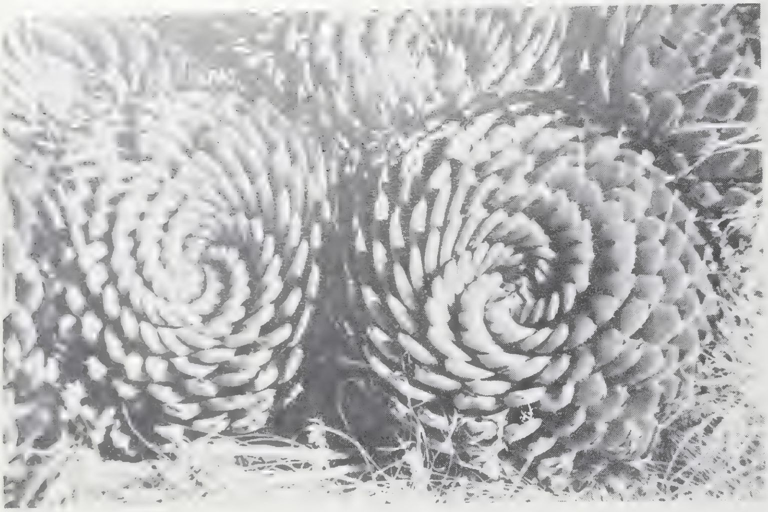

FIG. 1.—*Aloe polyphylla in situ.*

carrying out of the function and duties under this Act'.

On the advice of the PPC, the Minister of Education later issued a Legal Notice (No. 36 of 1969) where the Monuments, Relics, Protected Fauna and Flora in Act 41 were defined. The first item in the schedule of protected flora is concerned with aloes and *A. polyphylla* and its seeds and flowers are specifically mentioned.

FIELD EVIDENCE OF STATUS OF SPECIES

Evidence for the current status of the species from four fieldsites that have been monitored by various workers is given here. The type locality given by Reynolds (1950) is the western slope of an area known as Phurumela (Furumela), 50 km east of Maseru. This locality, quite close to a large trading store linked to the lowlands by road, was visited in 1958 by Schmitz who found a large number of aloes, but did not count them. In 1966 Ambrose (pers. com.) counted 293 plants at a lower site near a village, and 116 plants at an upper site near the mountain summit. When he went back there in 1973, no spiral aloes were left at the upper site. Schmitz was told in 1972 that two lorries full of *A. polyphylla* had been sold to 'a European'. Beverly also declared this site extinct in 1977 and could not find any evidence of regeneration from seeds that may have fallen on the ground from mature plants, long since removed or destroyed. The depletion of aloes from this site was noted by one of the sisters in the hospital at Roma, who knows this area well. At the lower site, *A. polyphylla* enjoys the protection of the village headman who is well aware that they have a cash value. According to Beverly, plant numbers were reduced to 102 by 1977.

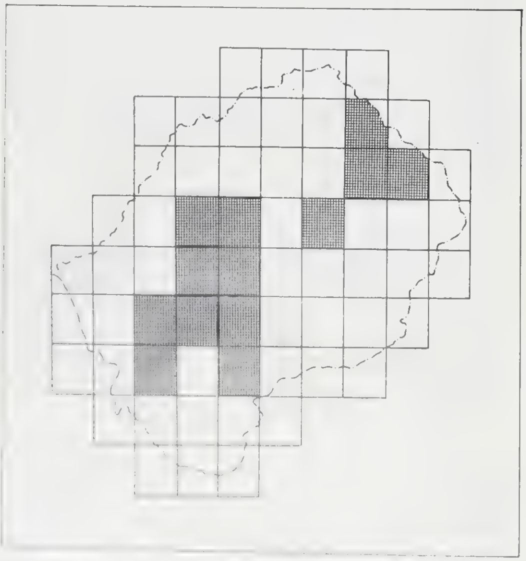

FIG. 2.—Known distibution of *Aloe polyphylla* within Lesotho. Each shaded quadrangle contains one or more confirmed sites. Data from Ambrose (pers. com.) & Beverly, 1978.

Another site, within motorable distance from Maseru and close to the Mountain Road, is also extinct. Visitors to Lesotho often take the spectacular drive into the mountainous interior of Lesotho up the Mountain Road, and have been offered spiral aloes for sale (Jacot Guillarmod, 1975). Some plants from here and from the type locality mentioned earlier may have found their way to the National University, where newly arrived staff members would buy this beautiful aloe, not knowing that they are protected. Recently, however, the number of sellers (Fig. 3) has decreased, presumably because the law prohibiting the sale of spiral aloes has become widely known, and also because there are so few left. The lifting of these plants for sale has by no means stopped, even now. Someone from Europe was sold one in Maseru in October 1980, shortly after arrival.

Other former sites, now exhausted, were similarly located within short distances from roads or motorable tracks, and stories of plants being carried away from hillsides on donkeys in sacks for transportation by lorry out of Lesotho are not uncommon. Beverly (1977) observed certain wanton

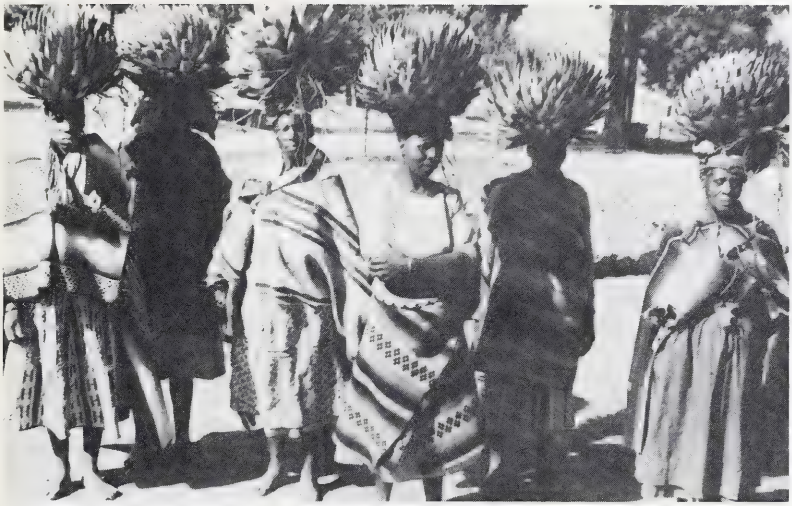

FIG. 3.—*Aloe polyphylla* on offer for sale at Roma, 1966. At the time, several sites now extinct were within walking distance of Roma. The women transport aloes on their heads, one at a time.

destruction as well. At a locality in Quthing district having 232 plants, 35 had been uprooted, some plants having been rolled down the hillside by herdboys and the inflorescence had been knocked off most plants. The result was that there were no seeds or seedlings. Such vandalism threatens the very existence of the species. The construction of the Southern Perimeter Road will have begun by mid-1981. It will pass through this area and the site will be further threatened.

One of the larger sites within easy reach by vehicles from the national capital, Maseru, has been kept under observation since 1976. The numbers counted by different observers are given in Table 1.

As observed by Ambrose and Talukdar, many plants had divided into a left-handed and a right-handed spiral, each of which produced a scape, or sometimes the scape arose from the point of division. In one case the scape arose at a point where the cheirality reversed in a single plant. The scape usually had 5–7 branches, but in one clump a plant with 14 branches was observed.

The number of plants is probably declining because of the removal of young plants from this site. There appears to have been no regeneration from seeds in the last three years. However, it must be remembered that November 1980 was very dry in Lesotho.

Flowers were at their best in early November, but some continue flowering up to a month after that (Fig. 6). (Cultivated plants occasionally flower for a second time in February–March.) Malachite sunbirds were observed sipping nectar from the long tubular flowers. Bees and hover flies also assist in pollination.

CONSERVATION STRATEGIES

Legislation, publicity and education

The Protection and Preservation Commission issued a Public Notice circulated in Lesotho in April 1970 prohibiting the removal and/or export of *Aloe polyphylla.* Authority to remove the spiral aloe can only be obtained from the PPC, and such permission will only be given for genuine educational or scientific purposes and not for commercial or other purposes.

TABLE 1.—Plant and seedling counts at one of larger sites of *Aloe polyphylla* in Lesotho

Year	Observer	Adult plants	Seedlings
1976	Beverly	300	10 (Schmitz)
1977	Schmitz	394	2
1977	Beverly	collected seeds	0
1979	Schmitz	was able to count on one face only; number was unchanged	0
1980	Ambrose & Talukdar	373 no young plants less than 40 cm in diameter; the largest plants were up to 110 cm in diameter	0

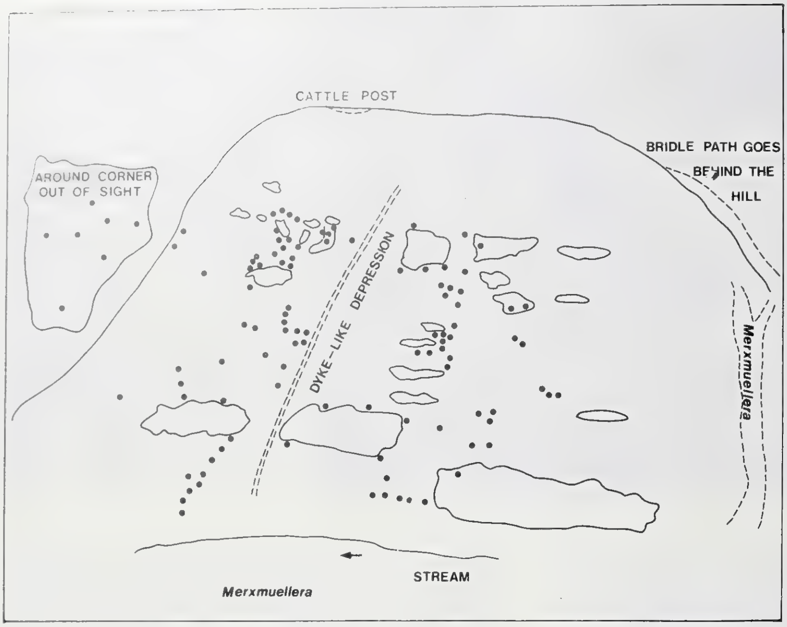

FIG. 4.—Sketch of the site where spiral aloe census was taken. It is a steep hillside of NW aspect, 2 450–2 500 m above sea level. Rocky outcrops are outlined and *A. polyphylla* clumps have been marked with black dots. The number of aloes per clump was from 1 to 8, one had as many as 12. They grow almost down to a stream with abundant tussocks of *Merxmuellera* on both sides. The soil is basalt-derived.

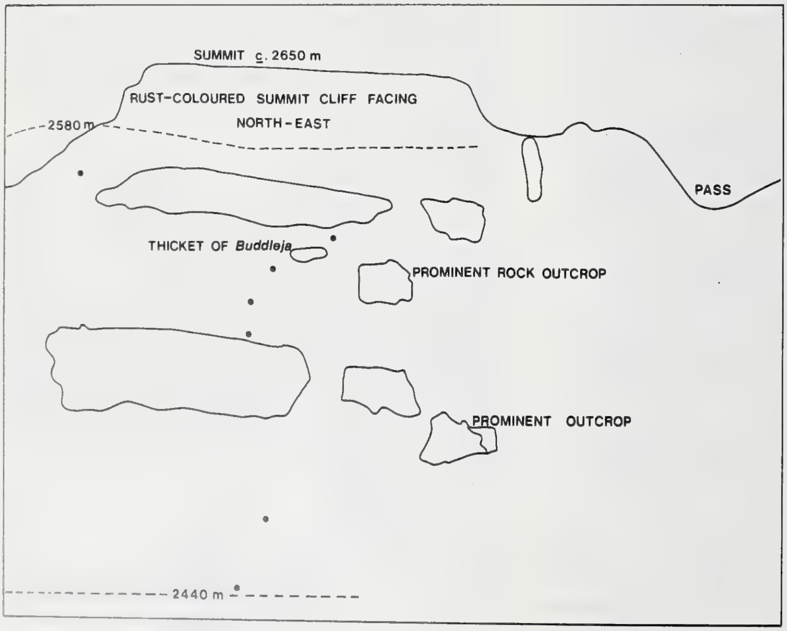

FIG. 5.—A smaller site with only 9 plants (altitude 2 450–2 550 m) seems to be a remnant protected by the steepness of the slope, and therefore inaccessible. There is a danger from intense grazing by goats and the destruction of soil cover. Black dot = *Aloe polyphylla* clump.

Act No. 41 of 1967 prescribed a fine of R200 or imprisonment not exceeding six months in default of payment (paragraph 12). Although many headmen and chiefs knew this, aloes continued to disappear. The PPC was concerned and decided that the protection of *A. polyphylla* should be one of its pilot projects (October 1968). A plan was drawn up with the following points:-

(1) That the aloe is protected must be publicized in all possible ways and the police alerted.

(2) Aloes removed without permission should be confiscated. The confiscated plants should be cared for in a safe place.

(3) A nursery to raise aloes from seeds should be started. These plants could be sold legally thus taking the pressure off natural sites. Plants raised in the nursery could be used for restocking exhausted sites.

The PPC has sought to pursue these lines of action, but it is handicapped by having no field

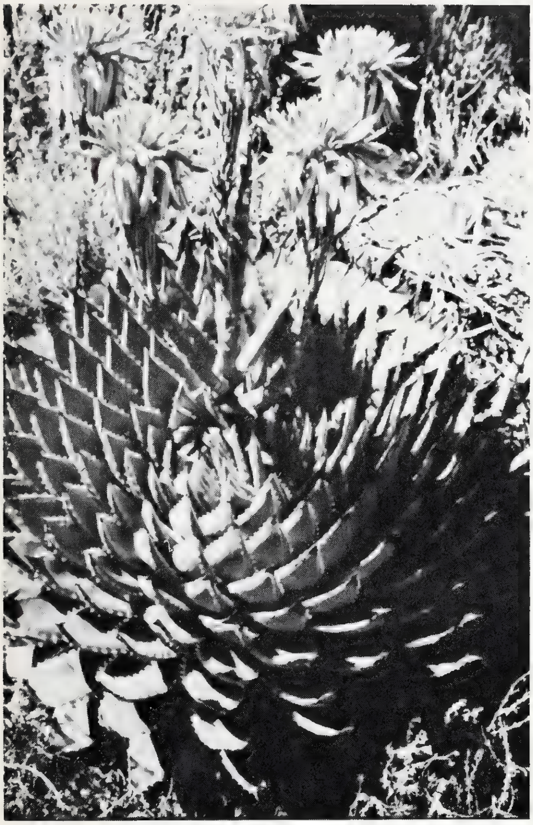

FIG. 6.—*Aloe polyphylla* flowering.

workers. The members hold full-time jobs elsewhere and can at the best, only advise. Unless there is an adequate budget and full-time field staff, these ideas cannot be implemented.

Aloe *nursery*

A nursery for spiral aloes was started in Maseru in 1977 by two officers of the Thaba-Bosiu Rural Development Project. It is now in charge of the Curator, Maseru Herbarium, in the Agricultural Research Division of the Ministry of Agriculture. Mrs Lerato Mohapi, the Curator, has successfully raised a number of spiral aloes from seed and has recently requested (1981) PPC's permission to sell some of these plants. In the process of growing them, much information has been gained on the growth of *A. polyphylla*. The physiology of seed germination would be an interesting research topic. The knowledge gained from this kind of research could be applied to solve the problems of restocking depleted sites. Its ecology under natural conditions, particularly its association with other plants (Fig. 7), will be another interesting line of investigation.

CONCLUSION

The conservation of spiral aloes is a matter of some urgency, and the measures initiated in Lesotho are showing some success, though much more needs to be done.

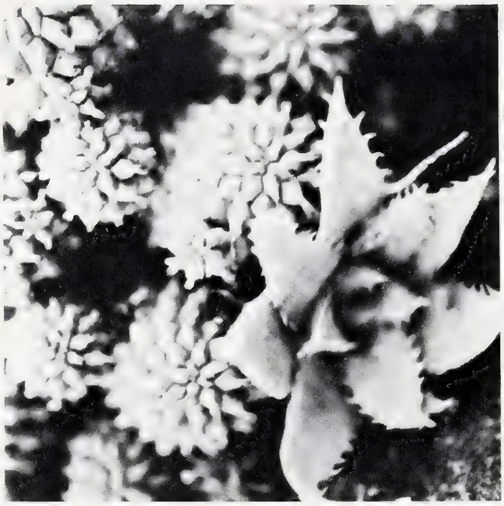

FIG. 7.—Association of *A. polyphylla* seedling in its natural habitat with *Euphorbia clavarioides*.

ACKNOWLEDGEMENTS

I wish to record my thanks to the members of the Protection and Preservation Commission who answered many questions and also to A. C. Beverly and L. Mohapi for interesting discussions on their observations. The help of D. P. Ambrose with the map is gratefully acknowledged. Thanks are also due to Dr R. H. Meakins of the Biology Department, National University of Lesotho, for rephotographing some of the colour transparencies; and particularly to the late Marthe Schmitz for her collaboration in the preparation of this paper.

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Bothalia 14, 3 & 4: 991–995 (1983)

The present status of vegetation conservation in South Africa

J. C. SCHEEPERS*

ABSTRACT

Progress with the conservation of representative stands of the great variety of South African ecosystems, as represented by vegetation types, is reviewed against progress towards better co-ordinated and national planning of the various conservation activities pursued by different conservation authorities.

RÉSUMÉ

LE STATUT ACTUEL DE LA CONSERVATION DE LA VÉGÉTATION EN AFRIQUE DU SUD

Les progrès obtenus dans la conservation de zones représentatives de la grande variété d'écosystèmes sud-africains, tels qu'ils sont représentés par des types de végétation, sont examinés en les comparant avec ceux réalisés pour établir un programme à l'échelle nationale et mieux coordonné des diverses activités de conservation poursuivies par différentes autorités responsables.

A great deal has happened during the sixteen years since the 1966 AETFAT meeting on 'Conservation of vegetation in Africa south of the Sahara'. This paper can only summarize the main developments, assess trends and attempt to derive conclusions regarding the present conservation status of vegetation in South Africa.

In the light of Hedberg's (1976) follow-up report, it is necessary to refer to the Uppsala meeting where Codd (1968) in his regional synthesis pointed out that greater co-ordination was needed between the various bodies concerned with conservation of indigenous vegetation. This is gradually coming about and will be referred to again.

At the 1966 AETFAT meeting, Rycroft, reporting on the situation in the Cape Province, recommended the creation of extensive nature reserves to conserve mountain fynbos, Karoo Succulent Steppe, Subdesert (Karoo Shrub and Grass), and subdesert Steppe, using the nomenclature of the AETFAT vegetation map (Keay, 1959).

Also using the AETFAT nomenclature, Killick, briefly described the five vegetation types in the Transvaal and discussed their conservation status at that time. He suggested that it would be far more desirable for conservation status of vegetation types to be assessed on the basis of Acocks's Veld Types (1975) rather than the vegetation types used in the AETFAT map. He recommended that each veld type should contain one or more reserves containing a representative stand of the veld type. This view immediately gained wide acceptance throughout South Africa. Killick also suggested that steps should be taken to conserve all forest — even on privately owned land.

Bayer, Bigalke and Crass similarly described the occurrence of the five AETFAT vegetation types in Natal, and discussed their conservation status. By implication, they also suggested that the AETFAT vegetation types were not sufficiently fine for assessing adequacy of conservation coverage. They recommended that protection be extended to suitable stands of swamp forest, mangroves, coast forest and dune forest.

Roberts discussed four AETFAT vegetation types found in the Orange Free State. He recommended that protection be given to the two main variations of wooded steppe (*Acacia* Savanna) equivalent to Acocks's Veld Type No. 16 (Kalahari Thornveld and Shrub Bushveld). He also recommended that a greater area should be conserved of the subdesert steppe (Karroid Grassland) of various types. As pointed out by Hedberg (1976), the latter need has been partially met by Tussen-die-Riviere Game Farm.

Against the foregoing historical background, a milestone was reached with the review of the status of conservation in the Republic of South Africa, being a South African contribution to Section CT (Conservation of Terrestrial Communities) of the International Biological Programme. While the investigations reported on were stimulated by the international programme, the accent of the review was on national rather than international needs. Of prime importance was the report of Edwards (1974), on a broad survey of the conservation status of South African vegetation. Statistical data and maps showed the distribution and total areas conserved by various conservation agencies, the size distribution of nature reserves, and the areas and percentages of conserved areas in relation to Acocks's 70 veld types and seven main vegetation types. Major conservation deficiencies lay in the Karoo and Karroid Bushveld and Grassland vegetation types, where 42 veld types had no or practically no conservation. In the Tropical Bush and Savanna Types, nine veld types were found to be extremely lacking in conservation. Additional reserves were seen to be needed to conserve certain important and local ecosystems and species in the remaining 18 veld types, especially the Sclerophyllous Bush (Fynbos) and Temperate and Transitional Forest and Scrub Types and in certain Coastal Tropical Forest and Thornveld Types. Apart from minor shortcomings, the conservation status was outstanding for six of

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these 18 veld types (up to 46 per cent conserved) and very good for another six veld types.

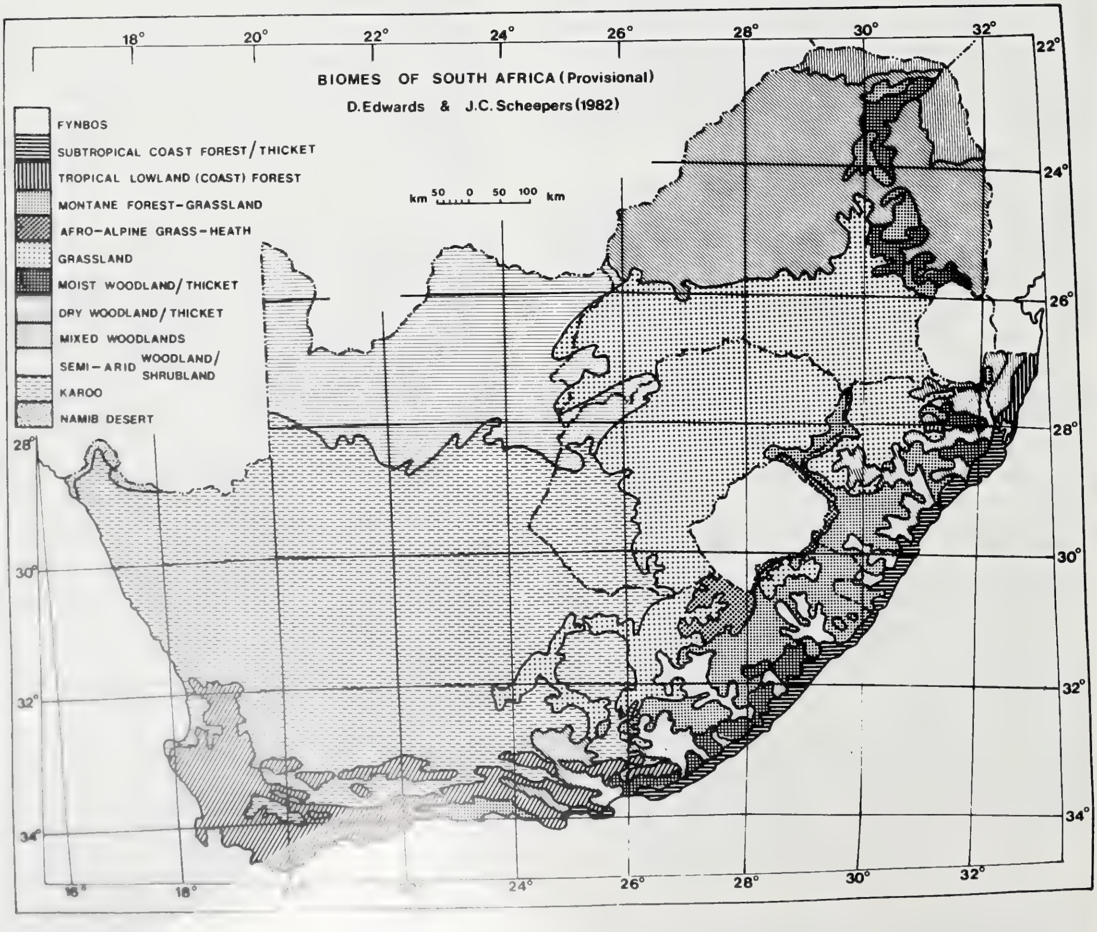
Meanwhile, the National Committee for Nature Conservation (NAKOR) had been established in 1963 to promote and co-ordinate nature conservation in South Africa through co-operation between all of the official nature conservation bodies, without in any way detracting from the autonomy of any of these bodies. NAKOR initiated a National Plan for Nature Conservation at the request of the then Department of Planning and the Environment (now the Department of Environment Affairs) that would integrate and co-ordinate the National Plan for Nature Conservation with other planning towards the National Physical Development Plan and regional development plans.

A series of questionnaires was drawn up and sent out to the conservation bodies concerned, and this exercise is repeated annually to update the National Plan. These questionnaires relate to existing permanent conservation areas, planned or proposed conservation areas, and remaining future conservation needs. The adequacy of existing and planned future coverage, and the remaining future conservation needs are assessed from different points of view, e.g. conservation of veld types, conservation of special plant communities, and conservation of special habitats of threatened species.

To date, facilities for the storage, retrieval and processing of data and for mapping have been provided by the Botanical Research Institute of the Department of Agriculture. Until recently the Botanical Research Institute provided the services of a part-time co-ordinator and part-time technical support. The Department of Environment Affairs now provides a full-time co-ordinator with supporting staff, as well as the Secretariat, and will soon assume responsibility for data processing and mapping.

The National Plan for Nature Conservation is an on-going project of an open-ended nature. The data base is annually updated, and maps and co-ordinated plans are reviewed at convenient intervals. Compilations of information derived from the questionnaires and maps are used at planning workshops to determine conservation priorities at national and provincial levels.

With regard to the conservation of vegetation, Table 1 provides a brief summary of the current



[illegible] map of the biomes of South Africa.

TABLE 1. – Percentage areas conserved of various veld types (NB. These statistics are based on questionnaire-derived data and are subject to error)

Veld Type No.	Area of Veld Type (ha)	Area of Veld Type conserved (ha)	Percentage of area of Veld Type conserved %
1	2 639 950,0	34 367	1,30
2	210 890,0	150	0,07
3	83 310,0	3 400	4,08
4	402 090,0	13 901	3,46
5	1 196 580,0	11 144	0,93
6	356 450,0	21 200	5,95
7	645 520,0	200	0,03
8	952 840,0	30 559	3,21
9	1 194 180,0	77 133	6,46
10	2 379 710,0	528 840	22,2
11	1 900 450,0	590 835	31,1
12	587 920,0	0	0
13	839 350,0	300	0,04
14	1 822 050,0	4 766	0,26
15	2 086 810,0	853 067	40,9
16	13 908 190,0	986 826	7,0
17	1 804 570,0	700	0,04
18	3 986 720,0	63 384	1,59
19	3 448 180,0	15 293	0,44
20	1 301 870,0	50 901	2,27
21	389 150,0	35	0,009
22	462 230,0	0	0
23	2 716 710,0	29 720	1,09
24	274 350,0	0	0
25	935 880,0	6 900	0,74
26	3 378 590,0	4 710	0,14
27	1 956 930,0	320	0,02
28	2 135 760,0	1 760	0,08
29	7 688 440,0	760	0,01
30	1 115 240,0	0	0
31	3 714 910,0	540	0,01
32	3 714 190,0	9 485	0,25
33	2 810 590,0	4 600	0,16
34	733 540,0	3 306	0,45
35	2 783 870,0	0	0
36	5 983 060,0	63 849	1,06
37	1 107 060,0	11 521	1,04
38	119 150,0	0	0
39	119 540,0	0	0
40	617 420,0	0	0
41	121 750,0	0	0
42	225 870,0	2 849	1,26
43	621 280,0	75 177	12,10
44	3 173 780,0	101 397	3,19
45	394 480,0	618	0,15
46	178 880,0	10 530	0,59
47	928 870,0	22 503	2,42
48	3 753 160,0	903	0,02
49	1 714 730,0	7 300	0,43
50	4 707 150,0	13 530	0,29
51	275 780,0	0	0
52	1 079 790,0	0	0
53	1 211 510,0	0	0
54	290 240,0	379	0,13
55	62 910,0	0	0
56	989 980,0	1 206	0,12
57	1 475 200,0	1 000	0,68
58	980 080,0	63 493	6,48
59	256 720,0	0	0
60	1 522 320,0	1 249	0,082
61	3 003 360,0	17 148	0,57
62	151 940,0	0	0
63	788 830,0	6 075	0,77
64	540 580,0	11 415	2,11
65	1 843 740,0	3 829	0,21
66	577 160,0	0	0
67	248 990,0	0	0
68	67 330,0	0	0
69	1 980 130,0	664 303	33,55
70	1 747 290,0	37 508	2,15

conservation status of veld types. The names of the various veld types are given in the Appendix. To facilitate understanding, the veld types are grouped into several biome types as mapped in Fig. 1. On this basis, the conservation status of the various biomes can be assessed (Table 2). An important point to remember in evaluating the conservation coverage of veld types is that a number of veld types, namely the so-called 'false' veld types of Acocks, are secondary, having been derived from the original natural vegetation as a result of overgrazing and trampling, over-burning, and also under-utilization and selective grazing. It would seem pointless to conserve and maintain these in their abused state by continued malpractice, failing which they will revert to the more natural condition, as is happening in the Tussen-die-Riviere Game Farm in the False Upper Karoo (Werger, 1973). From Table 2 it will be seen that the conservation status of the Grassland Biome, particularly the Highveld Grasslands, is particularly low. This is cause for grave concern owing to the serious threat posed by agricultural intensification and other developments.

To summarize the present position, it can be seen that, although changes have taken place since the survey of Edwards (1974), the general picture remains substantially the same as previously reported. The preponderance of conservation effort is concentrated in the veld types of the eastern and southern parts of South Africa. In contrast, almost negligible conservation is found in the semi-arid to arid western parts of the country.

Regarding the conservation of special plant communities, the information to date is patchy and reflects the fact that no standard acceptable list of special plant communities exists at present. Nevertheless, much interesting information has come to light but much more data are still required. The standardization of South African plant-community nomenclature is now receiving attention and this will help to systematize the conservation of special plant communities and put it on a sound footing.

With regard to Killick's report at the 1966 AETFAT meeting, the first step towards the all-embracing conservation of forest has been taken. The Wildlife Society of Southern Africa has launched a survey, enlisting the co-operation of its wide membership including predominantly the lay public, to ascertain the answers to the following questions: Where are all the forests on private land? What is their condition? Is their continued existence threatened in any way? What special features distinguish each forest? Which forests should be selected for conservation action? The Botanical Research Institute will provide professional and technical assistance where required. A report will be submitted to NAKOR in due course.

The position in regard to the conservation of threatened plant species gives cause for concern. A major handicap both for the official conservation agencies and for NAKOR in its function of co-ordinating conservation activities and plans, has been the lack, until recently, of an authoritative list of threatened plant species. The Working Group for Threatened Plant Species (of the Terrestrial Biology

TABLE 2. – Conservation status of South African biomes (with regional subtypes). The statistics are based on questionnaire-derived data and are subject to error

Biome – *Regional subtype* (with percentage area of South Africa and actual extent covered)	Area conserved ha	Percentage area conserved %
1. Fynbos biome (3,96%; 48 351,7 km^2)	734 844	15,19
(a) *Mountain Fynbos (& Forest)* (3,05%; 37 274,2 km^2) Veld types 69 & 70	701 811	18,8
(b) *Lowland Fynbos* (0,91%; 11 077,5 km^2) Veld types 46 & 47	33 033	2,98
2. Subtropical coast forest biome (1,42%; 116 434,9 km^2)	23 267	1,60
(a) *South-eastern* (1,2%; 14 326,0 km^2) Veld type 1 (south of St Lucia)	23 117	1,61
(b) *Southern* (Alexandria Forest) (0,17%; 2 108,9 km^2) Veld type 2	150	0,07
3. Tropical lowland (coast) forest biome *Veld type 1 (north of St Lucia)* (3.85%; 46 985,0 km^2)	115 916	2,5
4. Montane forest biome (2,74%; 33 466,7 km^2)	161 019	6,86
(a) *Montane* (0,91%; 11 139,5 km^2) Veld types 4,44 & 45	115 916	10,4
(b) *Submontane* (1,83%; 22 327,2 km^2) Veld types 3,5 & 8	45 103	2,02
5. Afro-alpine grass-heath biome (8,03%; 9 800,8 km^2) *(including Subalpine) Veld type 58*	63 493	6,48
6. South African grassland biome (20,7%; 243 124,3 km^2)	64 034	0,26
(a) *Eastern Grasslands* (3,07%; 37 503,1 km^2) Veld types 63, 64, 65 & 66	21 319	0,57
(b) *Highveld Grasslands* (16,84%; 205 621,2 km^2) Veld types 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 59, 60, 61, 62, 68	42 715	0,21
7. Moist woodland biome (including scrub and savanna intergrades) (1,8%; 21 961,5 km^2)	98 533	4,49
(a) *Eastern* (1,27%; 15 506,3 km^2) Veld types 6 & 9	98 333	6,34
(b) *South-eastern* (0,53%; 6 455,2 km^2) Veld type 7	200	0,03
8 Dry woodland biome (including scrub and savanna intergrades) (1,99%; 24 292,1 km^2)	860 884	3,5
(a) *Mopane* (1,71%; 20 868,1 km^2) Veld type 15	853 067	40,88
(b) Pteleopsis – Newtonia *Dry Forest/Thicket* (0,28%; 3 424,0 km^2) Veld types 1 & 10 (both in northern part of St Lucia)	7 817	2,28
9. Savanna biome (including scrub) (28,9%; 353 150,3 km^2)	227 160	6,43
(a) *Transvaal Bushveld* (9,4%; 114 796,7 km^2) Veld types 12, 13, 14, 18, 19, 20, 67	134 644	1,17
(b) *Eastern Transvaal Lowveld* (3,5%; 42 801,6 km^2) Veld types 10 & 11	1 119 675	26,16
(c) *Kalahari Scrub and Thornveld* (12,87%; 157 127,6 km^2) Veld types 16 & 17	987 526	6,28
(d) *South-eastern Karroid Scrub and Thornveld* (3,15%; 38 424,4 km^2) Veld types 21, 22, 23, 24	29 755	0,7
10. Karoo (26,27%; 320 759,48 km^2)	181 277	0,565
(a) *Succulent Karoo* (6,71%; 81 949,2 km^2) Veld types 25, 31, 33, 34, 39	11 206	0,137
(b) *Central Karoo* (13,37%; 163 241,38 km^2) Veld types 26, 27, 28, 29, 30, 32, 35, 40, 43	92 212	0,565
[illegible] *Grass Transition* (6,19%; 75 568,9 km^2)	77 859	1,03
11. Namib desert biome (0,167%; 1 313 km^2) [illegible] Veld types 31, 33 and 34 in vicinity of lower Orange River	8 446	6,43

Section of the National Programme for Environmental Sciences) has been working for several years to draw up a list of threatened plant species. This has now been published (Hall *et al.*, 1980) and a lead can be given to the conservation agencies. The list is essentially a first draft and much more research needs to be done before the conservation of threatened plant species can be planned and put into practice on a scientific basis.

In brief, while there are encouraging signs of progress, it is clear that the conservation status of the South African flora and vegetation is still deficient in a number of respects. To make good these deficiencies is a challenging and important task that will demand a great deal of hard work in the years ahead.

ACKNOWLEDGMENTS

I wish to express my grateful thanks to Dr S. S. du Plessis, Chairman of NAKOR, for permission to use statistics derived from the data bank of the NAKOR National Plan for Nature Conservation. I am also greatly indebted to Misses A. P. Backer and E. C. A. Smith for their help in preparing Tables 1 and 2.

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APPENDIX: VELD TYPES

I COASTAL TROPICAL FOREST TYPES
Veld Type No. 1 Coastal Forest and Thornveld
2 The Alexandria Forest
3 The Pondoland Coastal Plateau Sourveld
4 The Knysna Forest
5 The 'nGongoni Veld
6 The Zululand Thornveld
7 The Eastern Province Thornveld

II INLAND TROPICAL FOREST TYPES
8 North-eastern Mountain Sourveld
9 Lowveld Sour Bushveld

III TROPICAL BUSH AND SAVANNA TYPES (BUSHVELD)
10 Lowveld
11 Arid Lowveld
12 Springbok Flats Turf Thornveld
13 Other Turf Thornveld
14 Arid Sweet Bushveld
15 Mopani Veld
16 Kalahari Thornveld
17 Kalahari Thornveld Invaded by Karoo
18 Mixed Bushveld
19 Sourish Mixed Bushveld
20 Sour Bushveld

III A FALSE BUSHVELD TYPES
21 False Thornveld of Eastern Cape
22 Invasion of Grassland by Thorn

IV KAROO AND KARROID TYPES
23 Valley Bushveld
24 The Noorsveld
25 Succulent Mountain Scrub (Spekboomveld)
26 Karroid Broken Veld
27 Central Upper Karoo
28 Western Mountain Karoo
29 Arid Karoo
30 Central Lower Karoo
31 Succulent Karoo
32 The Orange River Broken Veld
33 The Namaqualand Broken Veld
34 Strandveld

IV A FALSE KAROO TYPES
35 False Arid Karoo
36 False Upper Karoo
37 False Karroid Broken Veld
38 False Central Lower Karoo
39 False Succulent Karoo
40 False Orange River Broken Veld
41 Pan Turf Veld Invaded by Karoo
42 Karroid *Merxmuellera* Mountain Veld Replaced by Karoo
43 Mountain Rhenosterbosveld

V TEMPERATE AND TRANSITIONAL FOREST AND SCRUB TYPES
44 Highland Sourveld and Dohne Sourveld
45 Natal Mist Belt 'nGongoni Veld
46 Coastal Rhenosterbosveld
47 Coastal Macchia

VI PURE GRASSVELD TYPES
48 *Cymbopogon–Themeda* Veld
49 Transitional *Cymbopogon–Themeda* Veld
50 Dry *Cymbopogon–Themeda* Veld
51 Pan Turf Veld
52 *Themeda* Veld or Turf Highveld
53 Patchy Highveld to *Cymbopogon–Themeda* Veld Transition
54 Turf Highveld to Highland Sourveld Transition
55 Bankenveld to Turf Highveld Transition
56 Highland Sourveld to *Cymbopogon–Themeda* Veld Transition
57 North-Eastern Sandy Highveld
58 *Themeda–Festuca* Alpine Veld
59 Stormberg Plateau Sweetveld
60 Karroid *Merxmuellera* Mountain Veld

VI A FALSE GRASSVELD TYPES
61 Bankenveld
62 Bankenveld to Sour Sandveld Transition
63 Piet Retief Sourveld
64 Northern Tall Grassveld
65 Southern Tall Grassveld
66 Natal Sour Sandveld
67 Pietersburg Plateau False Grassveld
68 Eastern Province Grassveld

VII SCLEROPHYLLOUS BUSH TYPES
69 Fynbos

VII A FALSE SCLEROPHYLLOUS BUSH TYPES
70 False Fynbos

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Isolating mechanisms among five sympatric species of *Aneilema* R. Br. (Commelinaceae) in Kenya

R. B. FADEN*

ABSTRACT

The reproductive biology and ecology of five non-hybridizing, sympatric species of *Aneilema* in Kenya is investigated. The high number of species at the study site is believed to be due to the ecological diversity at this locality. Differences in ecology and seasonal flowering periods appear to be inadequate to reproductively isolate these species. However, differences in daily flowering times, pollinators, floral morphology and opening behaviour, and in chromosome number, alone or in combination (perhaps also coacting with other factors not fully evaluated), are effective isolating mechanisms.

RÉSUMÉ

*MÉCANISMES D'ISOLATION PARMI CINQ ESPÈCES SYMPATRIQUES D'*ANEILEMA *R. BR. (COMMELINACÉES) AU KENYA*

*La biologie et l'écologie de la reproduction de cinq espèces sympatriques d'*Aneilema *qui ne peuvent s'hybrider sont étudiées au Kenya. Le nombre élevé d'espèces dans le site de l'étude est dû, croît-on, à la diversité écologique de cet endroit. Les différences dans l'écologie et dans la phénologie de la floraison paraissent être inadéquates pour isoler ces espèces par voie de reproduction. Cependant, des différences dans les durées journalières de la floraison, les agents pollinisateurs, la morphologie florale et le mode d'épanouissement, ainsi que dans le nombre chromosomique, ces facteurs considérés isolément ou combinés (peut-être aussi en association avec d'autres facteurs qui n'ont pas encore été complètement établis) constituent de réelles causes d'isolement.*

INTRODUCTION

The reproductive biology of species of Commelinaceae has been little studied in the field. This may be due to some of the following: there are relatively few species in temperate regions, e.g. none is native to Europe; taxa within the family are often difficult to identify even to genus; individual flowers are short-lived, and therefore plants are frequently encountered (or overlooked) in a nonflowering condition; reports in the literature of unusual reproductive syndromes in the family are scarce and obscure. The few records in the literature, e.g. Barnes (1949), the increasingly recognized diversity in floral morphology in the family as a whole and, in particular, within such recently studied genera as *Tripogandra* (Handlos, 1970, 1975) and *Aneilema* (Faden, 1975), and the accumulating information from observations of cultivated plants (Faden, unpublished; Owens, 1981) indicate that field studies of sexual reproduction in members of this family are likely to yield interesting data. In this paper reproductive characters of five species of *Aneilema* from one locality in Kenya are considered as potential isolating mechanisms among these taxa.

MATERIALS AND METHODS

In 1974, in the course of doing field work in Africa for a Ph.D. dissertation on *Aneilema* (Faden, 1975), we encountered five species of the genus at one locality in Kenya. Because this was the largest number of taxa found at any site, and four of the species belonged to the same section (section *Lamprodithyros*) of *Aneilema,* we decided to make detailed observations on the floral biology of these species.

The locality is in Kenya, K7, Tana River District, Garsen-Malindi road, 1,5 km towards Malindi from the turn off to Oda, 2° 32′S, 40° 07′30″E, altitude 5–15 m. Observations and collections were made between the 22nd and 24th of July, 1974. Buds for meiotic chromosome counts were collected in a mixture of chloroform, absolute ethanol and glacial acetic acid (4:3:1, v/v). Vouchers for the plants will be found at the Missouri Botanical Garden (MO) and other institutions. A set of bees and voucher slides for the chromosome counts are in the possession of the author. Some bee collections are in the Snow Entomological Museum, the University of Kansas.

The names used herein follow Faden (1975), with unpublished names in inverted commas: *A. hockii* De Wild. *(Faden & Faden* 74/1182); *A. petersii* (Hassk.) C. B. Clarke subsp. *petersii (Faden & Faden* 74/1183); *A. 'indehiscens'* Faden subsp. *'indehiscens' (Faden & Faden* 74/1184); *A. 'tanaense'* Faden (*Faden & Faden* 74/1185); *A. 'succulentum'* Faden (*Faden & Faden* 74/1186).

SITE AND HABITATS

The site straddles the present Garsen-Malindi road and the old alignment which is parallel to and east of it. Three distinct habitats occur. To the west of the new road, and abutting almost on it, is *Euphorbia robecchii–Commiphora boiviniana–Strychnos decussata* bushland (habitat 1). The soil is sandy, well-drained and there are scattered termite mounds. Some other characteristic species are *Calyptrotheca teitensis* (Pax & Vatke) Brenan, *Ochna inermis* (Forssk.) Schweinf. and *Vitex* sp. ?

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TABLE 1. – Ecological and reproductive characters of five sympatric species of *Aneilema* in Kenya

Character	*Aneilema hockii*	*Aneilema petersii* subsp. *petersii*	*Aneilema 'indehiscens'* subsp. *'indehiscens'*	*Aneilema 'tanaense'*	*Aneilema 'succulentum'*
Habitats[1]	2	1 & 2	1, 2 & 3	2 & 3	1 & 2
Exposure	full sun	shade or partial shade	shade or partial shade	partial shade	shade in 1, full sun in 2
Abundance	common	common in 1, locally common in 2	local & uncommon	common in 3, local & uncommon in 2	locally common
Habit	perennial	perennial	perennial	annual	perennial
Flowering condition	mature flowering, some mature fruits	mostly early flowering, no mature fruits	mostly early flowering, few mature fruits	mostly pre-flowering, few mature fruits	mostly early flowering, few mature fruits
Flower types present	pistillate, perfect, staminate	perfect, staminate (most)	perfect, staminate (few)	perfect, staminate	perfect, staminate (few)
Flower width (mm)	(18–)24–30	15–19	14,5–16	10–14,5	9–14
Paired petal colour[2]	very pale lavender, basal white 'V' (85D)	lilac (87D)	white	pink (84B–C, 84C)	very pale lilac (76C–D)
Flower scent	fragrant	none	none	none	none
Lateral stamen position	divergent	crossed	parallel	divergent	parallel
Lateral stamen filament length[5]	dimorphic	uniform[6]	uniform[6]	uniform[6]	dimorphic
Medial stamen pollen fertility[3,4]	sterile	fertile	fertile	fertile	fertile
Flowering times (h)	0615–1330	0556–1130	0600–1230	0830–1330	1150–1515
Speed of flower opening	slow	slow	slow	rapid	rapid
Lateral stamen retention[1]	not retained	not retained	not retained	retained	retained
Compatibility[4]	self-incompatible	self-incompatible (?)	self-compatible (?)	self-compatible	self-incompatible (?)
Autogamy[4,7]	–	– (?)	–	+	–
Chromosome number	$n = 16$	$n = 13$	$n = 26$	$n = 13$	$n = 13, 2n = 26$[8]

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[1] See text.

[2] Figures in parentheses are based on the *Royal Horticultural Society Colour Chart* (1966).

[3] Based on staining ability with cotton blue.

[4] Determined from populations of these taxa other than those at the study site.

[5] Dimorphic = lateral stamen filaments longer in staminate than in perfect flowers and in perfect than in pistillate flowers (if present); uniform = lateral stamen filaments not noticeably different in length in the different flower types.

[6] Stamen filaments were not measured, so a very slight dimorphism could have been overlooked.

[7] Based on observed fruit set: autogamous (+), xenogamous (–).

[8] Mitotic count from plants in cultivation.

nov. (*Faden & Faden* 74/1191.) Two Commelinaceae, a coastal form of *Commelina africana* L. and *Cyanotis* sp. 'A' of Faden & Suda (1980), are restricted to this habitat.

East of the old alignment and somewhat removed from it is *Commiphora campestris — Acacia bussei* bushland (habitat 3). This habitat differs from habitat 1 both in species composition and soil type. Some distinctive species are *Thespesia danis* Oliv., *Combretrum hereroense* Schinz, *Grewia tenax* (Forssk.) Fiori, *Maerua* sp. 'C' of FTEA, *Lannea greenwayi* Kokwaro and *Sansevieria powellii* N. E. Brown. The soil is a seasonally waterlogged, black cotton clay mixed with some sand. Termite mounds are absent.

Between habitats 1 and 3, and including all of the area between the two road alignments, is a greatly disturbed, mostly open habitat that was originally cleared as a right-of-way for telephone lines and is here designated as habitat 2. Some scattered shrubs and trees, e.g. *Thespesia danis,* and occasional patches of thicket occur, but the area is characterized by a great diversity of herbs which are mostly absent from the other two habitats. Examples include *Ipomoea mombassana* Vatke, *Portulaca* spp., *Endostemon tereticaulis* (Poir.) Ashby, *Chloris roxburghiana* Schult., *Abutilon guineense* (Schumach.) Bak. f. & Exell and the Commelinaceae *Aneilema hockii, Commelina erecta* L., *C. benghalensis* L., *C. forskalaei* Vahl. *C. imberbis* Hassk. and *C.* sp. aff. *erecta* L. (*Faden & Faden* 74/1187). The soil is similar to that of habitat 3, but with some admixture of sandy soil near the new road. A drainage line is present on the western side of habitat 2, parallel to the roads and closer to the new alignment. Termite mounds are also absent in this habitat.

ECOLOGICAL ISOLATION

Differences in ecology may effectively isolate sympatric species. From Table 1 it may be seen that only three of the five species occur in habitat 1 and only two of the five in habitat 3. Although all five species are present in habitat 2, *A. hockii* and *A. 'succulentum'* occur in open, sunny spots in this habitat, whereas the other three species are found in shade or partial shade. *Aneilema petersii* subsp. *petersii* grows mainly in sandy soils. It is at least as common in habitat 1 as it is in habitat 2. *Aneilema 'tanaense',* in contrast, grows chiefly in clayey soils. It is the only *Aneilema* which is most common in habitat 3.

From these data it appears that each of the species, with the possible exception of *A. 'indehiscens',* has a preferred habitat. The large number of *Aneilema* species at this locality is clearly due to the variety of habitats present. The occurrence of all five taxa in habitat 2 suggests that differences in habitat preference may not be sufficient in themselves to reproductively isolate species.

TEMPORAL ISOLATION

Species can be temporally isolated by flowering either during different seasons of the year or at different times of the day. In this part of Kenya highly seasonal rainfall separated by long dry periods causes related species to flower at the same time of year. Some phenological differences in flowering condition were noted among the five *Aneilema* species (Table 1). *Aneilema hockii* was clearly most advanced in flowering, and all four perennials were more precocious than the annual *A. 'tanaense'.* Yet, overall, these phenological differences appeared to be slight — four of the five species had at least a few mature fruits — and seasonal differences in flowering would seem to be ineffectual as isolating mechanisms at this site.

Non-overlapping daily flowering times can very effectively isolate species. Even partial temporal separation of flowering can greatly reduce the probability of interspecific pollen transfer. Among the *Aneilema* species at this locality, there are examples of both total and partial reproductive isolation by means of differences in flowering times (Table 1; Fig. 1). The daily flowering times of *Aneilema petersii* subsp. *petersii* and *A. 'succulentum'* do not overlap at all. The flowering times of *Aneilema 'indehiscens'* and *A. 'succulentum'* overlap briefly thereby probably effectively isolating these species. The situation for *A. 'tanaense'* is more complex. Its flowering time overlaps with all of the other species, but its flowers open some two and a half hours later than the three early-opening species. Similarly, although *A. 'tanaense'* and *A. 'succulentum'* have a combined flowering period of six and a half hours, they flower simultaneously for only about one and a half hours.

REPRODUCTIVE ISOLATION BY POLLINATORS

Whether partially overlapping flowering times function to isolate species depends mainly upon the behaviour of the insects which visit the flowers. From Table 2 it can be seen that each of the four *Aneilema* species on which bees were observed — no other potential pollinators were noted — was visited principally by one genus (and one species?) of bees. *Aneilema hockii* and *A. petersii* subsp. *petersii* shared the same principal pollinator, whereas *A. 'tanaense'* and *A. 'succulentum'* were visited mainly or exclusively by other bee genera. *A. 'tanaense',* however, was occasionally visited by *Amegilla*, the main pollinator of *A. hockii* and *A. petersii,* so pollen transfer among these three species would appear possible. *Aneilema 'succulentum'* shared no bee visitors, and this species was thereby reproductively isolated from the other three taxa. During the observation period, the flowers of *A. 'indehiscens'* had pollen removed from the anthers by 0850 h, but the pollinator was not observed.

REPRODUCTIVE ISOLATION BY FLORAL MORPHOLOGY

Differential visits by pollinators to related sympatric species may be due to differences in floral morphology. The flowers of all five species present at this locality differ among themselves in numerous attributes, such as size, petal colour, scent, position of lateral stamens at anthesis, fertility of the medial

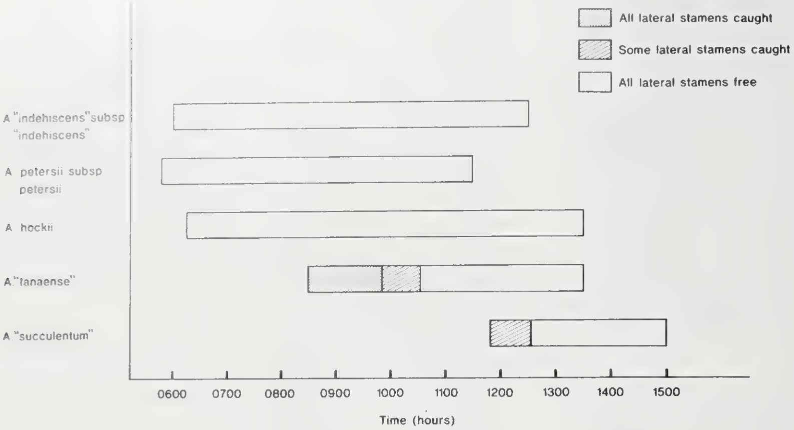

FIG. 1.—Flowering times of five sympatric species of *Aneilema* in Kenya.

stamen pollen, and the presence or absence of lateral stamen filament dimorphism in the different types of flowers (Table 1). How these various differences affect pollination are largely unknown, but a few generalizations may be made. Based on numerous observations made in 1974 of bees visiting several *Aneilema* species, including *A. hockii* and the annual subspecies of *A. petersii*, in the vicinity of Tsavo National Park East, Kenya, it appears that medium to large bees, e.g. *Amegilla,* preferentially visit flowers in which the stamens extend forwards to a considerable degree. At the present study site such species would be *A. hockii, A. petersii* and *A. 'indehiscens'*, which also happen to have the largest flowers. Smaller bees (< 10 mm long), e.g. *Lasioglossum, Nomia* and *Nomioides,* are most often observed visiting smaller-flowered species, e.g. *A. 'tanaense'* and *A. 'succulentum'*. They may also visit larger-flowered species, but in those flowers they frequently fail to make contact with the stigmas.

The position of the lateral stamens at anthesis determines the manner in which a flower can be 'worked' by visiting bees and also which part of the bee's anatomy is dusted with pollen. Larger bees visiting *A. hockii* flowers (Fig. 2.1) frequently grasp the long, divergent stamen filaments near the base and draw them together while backing towards the anthers (and usually contacting the stigma), so that the pollen of both lateral stamens can be collected simultaneously. The crossed lateral stamen filaments of *A. petersii* (Fig. 2.2) cause the pollen of these anthers to be presented in a direction different from that of all other species of the genus.

The avoidance of the flowers of certain species by particular bees may be wrongly attributed to an 'unworkable' floral morphology. It may be due instead to the opening of the flowers of completely unrelated taxa. *Amegilla* was seen visiting flowers of *Abutilon guineense* at 1216 h, just after they had opened, and also the flowers of *Plectranthus longipes* Bak. at 1640 h. This bee may not have been 'avoiding' *A. 'succulentum'* because its flowers were unattractive or difficult to manipulate, but merely because they were less attractive or rewarding than those of other available species.

TABLE 2.—Visits by bees to *Aneilema* species in a mixed colony in Kenya

Species of *Aneilema*	Bee [1]	Frequency of visits
A. hockii	*Amegilla* sp. [2] (Anthophoridae, Anthophorinae)	numerous
	Undetermined, uncollected bee	twice
A. petersii subsp. *petersii*	*Amegilla* sp.	very numerous
	Xylocopa or *Bombus* sp.? (not collected)	once
A. 'indehiscens' subsp. *'indehiscens'*	Not observed	
A. 'tanaense'	*Lasioglossum* sp. (Halictidae)	frequent
	Amegilla sp.	occasional
A. 'succulentum'	*Nomia* sp. (Halictidae)	numerous
	Nomioides sp. (Halictidae)	once

[illegible] may well belong to a single species.

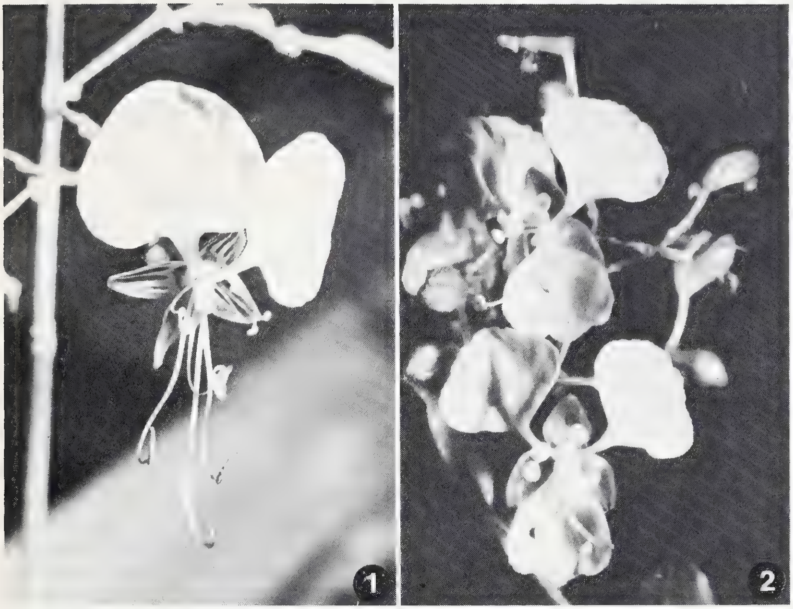

FIG. 2.—Flowers of: 1, *Aneilema hockii* De Wild., × 1,9, from *Faden et al.* 72/234; 2, *A. petersii* (Hassk.) C. B. Clarke subsp. *petersii* × 2,3 with staminate flower above and perfect flower below (from *Andrews* s.n.).

REPRODUCTIVE ISOLATION BY FLORAL OPENING BEHAVIOUR

If all of the pollen produced by a flower in which pollen is the sole floral reward is made available to insects at the same time, then most of that pollen may be collected soon after the flower opens, and the flower may not again be visited by potential pollinators. When the flowers open in certain species of *Aneilema* section *Lamprodithyros,* the lateral stamens are retained within the cup-shaped medial petal by its involute margins (Fig. 3.1). The margins of this petal gradually unroll and, when the margins are sufficiently far apart, the lateral stamens pop out, either singly or together (Fig. 3.2). The period of stamen retention varies from species to species. In the most extreme case, *A. calceolus* Brenan, both lateral stamens are held in the medial petals of all flowers for at least two hours, or more than half of the entire flowering period. In all cases the medial stamen is always free and available to insects from the time the flowers open.

The stamen retention mechanism may function in several ways: to increase outcrossing, to prolong the period during which the flowers are attractive to pollinators, and as an isolating mechanism. Outcrossing is promoted by the presentation of only a fraction of the flower's total pollen at a given time. This forces the insect to visit more flowers in order to obtain its needs. Attractiveness to pollinators is prolonged by the flower's pollen being presented over a period of time, so that it cannot all be collected when the flower opens. Stamen retention may serve as an isolating mechanism if any of the following are true: prolongation of pollen presentment leads to visitation by different species of bees (e.g. species which are active later) or effective temporal separation of flowering from related species; pollen presentment in smaller quantities per unit time selects for smaller bees.

Four of the five species at this locality — all but *A. hockii* — belong to section *Lamprodithyros.* Stamen retention is absent (apparently primitively)

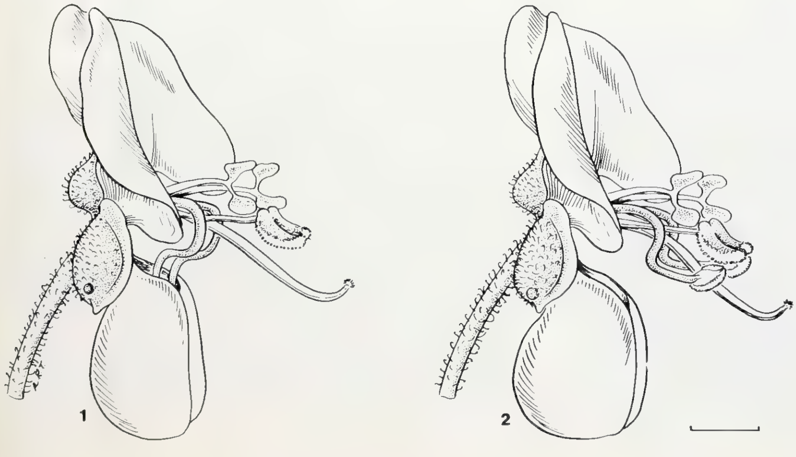

FIG. 3.—Flower of *Aneilema 'tanaense'* Faden. 1, lateral stamens retained in medial petal; 2, lateral stamens after release from medial petal. (From *Faden & Faden* 77/582.) The bar is 2 mm long.

TABLE 3.—Reproductive isolating mechanisms among five sympatric species of *Aneilema* in Kenya

	A. hockii	*A. petersii* subsp. *petersii*	*A. 'indehiscens'* subsp. *'indehiscens'*	*A. 'tenaense'*
A. 'succulentum'	flower size pollinator basic number	flowering time flower size pollinator	flowering time flower size ploidy	flowering time? pollinator
A. 'tanaense'	flower size basic number	flower size	flower size ploidy	
A. 'indehiscens' subsp. *'indehiscens'*	basic number ploidy	ploidy		
A. petersii subsp. *petersii*	basic number			

in *A. petersii* subsp. *petersii* and *A. 'indehiscens'* subsp. *'indehiscens'*, well developed in *A. 'tanaense'*, and poorly developed and seemingly disappearing — perhaps it is no longer needed? — in *A. 'succulentum'* (Fig. 1). The effect of these differences remains to be tested.

REPRODUCTIVE ISOLATION BY BREEDING SYSTEM AND CHROMOSOME NUMBER

Interspecific, incompatible pollen/stigma reactions can completely isolate species reproductively. Chromosomal incompatibility can also prevent hybridization. For all five species some data are available on self-compatibility, and on the presence or absence of autogamy (Table 1). Unfortunately, no crossing experiments among these species have been conducted, so it is not known whether cross-compatibility barriers exist. Chromosome numbers have been determined for all five species at this site (Table 1). Because *A. hockii* was found to differ in basic number from the other four species, and *A. 'indehiscens'* subsp. *indehiscens'* was discovered to differ in ploidy from the other three taxa which have the basic number $x = 13$, it is probable that reproductive isolation occurs between these two species and the other three taxa.

SUMMARY AND CONCLUSIONS

The occurrence of five species of *Aneilema* at a locality in Kenya, the largest number of species of the genus found at a single site, is analysed from the viewpoints of why so many taxa are present at this spot and how hybridization is prevented. The species are found to be somewhat distinct in their habitat preferences. It is concluded that the diversity of habitats is responsible for the unusually large number of *Aneilema* species present at this locality.

Reproductive isolation among these species is achieved by various means. The daily flowering times of some taxa do not or only barely overlap. Dissimilarities in floral morphology among the species, perhaps in conjunction with the variation in flowering times, result in certain species being visited by different genera of bees, the only pollinators observed. The variable morphological characters include the shape of the medial petal which in certain species of section *Lamprodithyros* retains the lateral stamens for specific periods of time after the flowers open, a possible isolating mechanism. Differences in basic chromosome number or ploidy probably reproductively isolate some of the taxa. All of these characters alone or in combination, and probably others which cannot yet be evaluated, effectively isolate these five species at this locality. No hybrids were found (Table 3).

ACKNOWLEDGEMENTS

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Nocturnal petal movements in the Asteraceae

C. H. STIRTON*

ABSTRACT

Nocturnal petal movements were recorded from 48 genera and 106 species growing in cultivation at the Royal Botanic Gardens, Kew and in the wild in Canada, Great Britain, France, Italy, Greece, Canary Islands and South Africa. Seven different night positions of petals, as distinct from day positions, are recognized and discussed.

RÉSUMÉ

LES MOUVEMENTS NOCTURNES DES PÉTALES DES ASTÉRACÉES

Des mouvements nocturnes des pétales ont été observés dans 48 genres et 106 espèces croissant en culture dans les Jardins Botaniques Royaux de Kew et en pleine nature au Canada, en Grande Bretagne, France, Italie, Grèce, aux Iles Canaries et en Afrique du Sud. Sept positions nocturnes différentes des pétales, distinctes des positions diurnes, sont reconnues et discutées.

INTRODUCTION

One of the great differences between plants and animals is that animals are mostly mobile, whereas plants are essentially static organisms. When plants do move, the movements are usually restricted to a particular organ or group of organs. Such movements are usually subtle and slow, or rapid and unexpected. It is these two qualities of plant movements that have fascinated naturalists for hundreds of years and, as this paper is evidence, continue to do so today.

Although the study of flower movements, or anthokinetics, as some prefer to call it (Goldsmith & Hafenrichter, 1932), has been carried out by amateur naturalists and professionals alike, little attention has been given to the phylogenetic significance of such movements. Such studies have established the variability and frequency of movements of flowers and flower parts, but have scarcely considered their ecological importance or their evolutionary and adaptive significance.

Such ideas were very far from my mind when I made my first observations on petal movements in the Asteraceae. The earliest observations were merely visual impressions, but ones which gradually coalesced into discernible phenomena. It became clear to me that the asteraceous capitulum is a complex structure with many interacting functions and that a cursory inspection of any single component is fraught with pitfalls if generalizations are to be drawn from data gathered about them.

This can be seen very clearly in the work of Leppik (1977). According to Leppik the most attractive floral patterns and specialized pollination mechanisms in the Asteraceae have co-evolved with the sensory development of their pollinators. However, as Burtt (1975, 1977) has so clearly noted, the structure of the capitulum has to meet the demands of both the flowering and the fruiting phases, and not, as Leppik (1977) suggests, the flowering state only.

It seems clear that if we are to understand the adaptive significance of structures and their functions, we need to view the flower and inflorescence/infructescence as evolutionary compromises between inherent genetic constraints and those constraints acting from outside the plant (Polhill, Raven & Stirton, 1981). This requires a closer look at the complex relationships that occur between component parts, how these change in position and function during their different developmental stages and how during such development they may combine in different sequences.

The study of floral movements in the Asteraceae has already provided fascinating information, for example, irritability of the pollen-presentation mechanism (Small, 1919), and involucral movements (Burtt, 1977). The present study continues in this tradition and, although a long-term study is needed before generalizations can be drawn of the type discussed above, enough data has been collected to warrant a preliminary descriptive report.

MATERIAL AND METHODS

Data were recorded from plants growing both in the wild and in cultivation. Notes were made of the position of petals one hour before sunrise, six hours after sunrise, just before sunset and finally, one hour after sunset. The majority of the species studied were growing in open cultivation in order-beds at the Royal Botanic Gardens, Kew, and were observed in two different summers, 1978 and 1979. The remaining observations were made on plants growing in the wild in Canada, Great Britain, France, Switzerland, Italy, Greece, the Canary Islands and in southern Africa. Only the movements of ligulate florets were recorded, and care was taken to avoid older flowers as in these some petals begin to adopt senescent positions which are often quite different from the night positions.

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RESULTS

The movement of ligulate florets towards their night position begins just before or just after sunset and may take one quarter of an hour to three hours to complete. Likewise, their return to the daylight position occurs predominantly after sunrise, often as late as mid-morning.

Although seven different night positions have been found (Fig. 1.1–1.7) and figured, I have also seen three others, two of which occur in *Gazania.* In some species the individual petals remain horizontal or rise somewhat vertically as in Position 3 but, instead of remaining flat, the petal margins roll either inwards or outwards (Fig. 1.8). Finally, I recall seeing an endemic daisy in the Canary Islands, in which the petals rolled upwards until they rested on top of the capitulum (Fig. 1.9), that is, the opposite of Position 1.

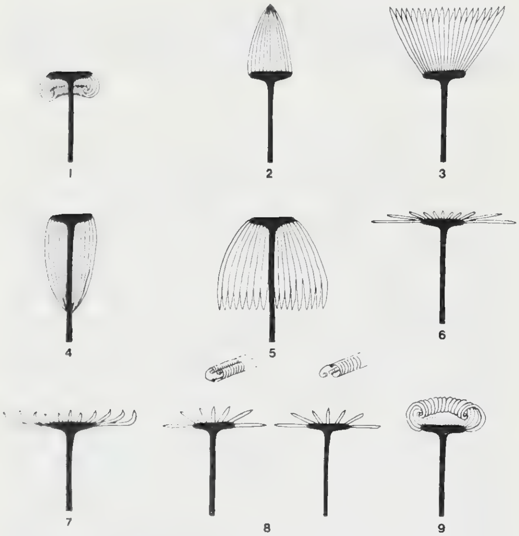


FIG. 1.—Nine basic night positions of ligulate petals in capitula of Asteraceae.

The three commonest night positions are numbers 1, 2, 4 and 5 respectively (Table 1.). Position 2 is significantly more widespread than any other position and occurs in the tribes Anthemideae, Arctoteae, Astereae, Inuleae and Lactuceae. Some tribes appear to be charaterized by a single position, for example, position 2 in the Lactuceae, Arctoteae, Cynareae and Calenduleae, whereas in other tribes such as the Anthemideae and the Heliantheae three to five positions may be adopted.

Broadly speaking, each genus appears to have a definite and characteristic night position. Exceptions are *Argyranthemum*, *Chrysanthemum* and *Erigeron* which all have two types of night positions. No species have been found which adopts more than one night position.

DISCUSSION AND CONCLUSIONS

The involucre is perhaps the most important organ of [illegible] and external stimuli. Burtt (1977) lists five functions of the involucre which, if considered ecologically, all involve anthokinesis. These include the protection of young flowers, the protection of mature flowers at night or during inclement weather, the attraction of pollinators, the protection of developing fruits, and the release of ripe achenes, or their enclosure and dispersal as a unit.

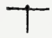
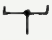
The second most obvious organ that is anthokinetic is the corolla. As we have seen these movements are most pronounced in ligulate corollas. Although these are often synchronous with involucral movements, they usually occur at night or during the day under certain environmental conditions. It is perhaps significant that those capitula which have weakly developed involucres are often protected by the shift of the protective role from the involucre to the enlarged outer ligulate corollas. For example, in *Gazania* the involucre is robust and dominates opening and tight closure of the flowers, whereas in some of the Calenduleae the petal movements are more dominant. Ligulate petals also help in the attraction of pollinators, in their own right, or by exposing or camouflaging the UV-absorbent disc florets. Such day-time movements may have parallels with the night movements. Is it possible that Positions 3, 6, 7 may be involved with moth visitation?

A dominant feature of many Asteraceae are their brightly coloured flowers often of intense yellow and orange hues. Is it possible that the ligulate florets of these colours are warning devices against herbivores and not as is generally accepted, attractants for pollinators? Can they be a combination of both? And what about the deep purpling often present on the undersurface? Does this assist in camouflage when the flower is closed? Has it a protective role in preventing damage by UV-radiation? Involucres may also be brightly coloured and/or deeply purple on their outer surfaces and so have similar attractive and/or protective roles.

These few observations and comparisons between the involucre and ligulate florets suggest that only careful observations that discriminate how and what functions are shifted from one organ to another will be useful in drawing generalizations of biological significance.

Differences between the day and night positions of ligulate florets strongly suggest that the day positions are related more closely to herbivore avoidance, pollinator attraction and protection against inclement weather. The common phenomenon of sun-tracking, considered together with the dusk and dawn movements, strongly implicate light and temperature as prime causal stimuli. Baagoe (1977) has remarked particularly on the constant occurrence of highly specialized ligule epidermis types within different taxa and suggests that they must be 'genetically fixed functional adaptations rather than ontogenetically developed structural eventualities'. Her data is fully supported by Kay, Daoud & Stirton (1981) and Stirton (1981). Although it is still too early to draw any conclusions about the possible correlation of floral movements and the microstructure of floral parts, there does

TABLE 1.—Distribution of different night positions of petals in ligulate florets of Asteraceae according to tribes and genera

Tribes / Genera	Number of species found with each type of movement							Number of species
	1	2	3	4	5	6 	7 	
1. *Anthemideae*								
Achillea			2					
Anacyclus		1						
Anthemis				3				
Argyranthemum				4	1			
Chrysanthemum				8		2		
Leucanthemum				2				
Ursinia		1						24
2. *Arctoteae*								
Arctotis		1						
Berkheya		1						2
3. *Arniceae*								
Arnica					1			1
4. *Astereae*								
Amellus	1							
Aster		2						
Bellis		1						
Brachycome	1							
Calotes	1							
Chareis	1							
Erigeron	2	2						
Grindelia		2						13
5. *Calenduleae*								
Calendula		3						
Dimorphotheca		2						
Osteospermum		1						6
6. *Cynareae*								
Carduus		1						
Centaurea		1						2
7. *Heliantheae*								
Bidens						1		
Coreopsis					3			
Helenium					2			
Helianthella					1			
Sanvitalia					1			
Tridax					1			
Verbesina							1	10
8. *Inuleae*								
Helipterum		3						3
9. *Lactuceae*								
Andryala		1						
Cichorium		2						
Crepis		5						
Hedypnois		1						
Hieracium		9						
Hyoseris		1						
Hypochoeris		1						
Lactuca		4						
Leontodon		2						
Picris		2						
Scolymus		1						
Tolpis		2						
Tragopogon		1						
Urospermum		2						34
10. *Mutiseae*								
Perezia	1							1
11. *Senecioneae*								
Ligularia	7							
Senecio					2			9
12. *Tageteae*								
Tagetes					1			1
TOTALS 48 genera	14	56	2	17	13	3	1	106

seem to be ground for further investigation, particularly with respect to diurnal movements, not recorded here, but which are essentially the same as nocturnal movements and usually correlated to low periods of pollinator foraging. The possibility that those daisies which remain open at night could be moth pollinated should similarly be investigated.

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Speciation environments and centres of species diversity in southern Africa: 2. Case studies

G. E. GIBBS RUSSELL* and E. R. ROBINSON**

ABSTRACT

Distributions of species in the grass genera *Cymbopogon, Digitaria, Ehrharta* and *Stipagrostis* are mapped to show that speciation within the phytochorion, where a genus has undergone major adaptive radiation ('phytochorial sympatry'), may be differentiated from speciation in a phytochorion outside this characteristic one ('phytochorial allopatry'). Testing of this hypothesis seems a fruitful field for systematists and will enhance our understanding of the flora.

RÉSUMÉ

MILIEUX DE SPÉCIATION ET CENTRES DE DIVERSITÉ DES ESPÈCES EN AFRIQUE DU SUD. 2. ETUDES PARTICULIÈRES.

Les répartitions geographiques des espèces dans les quatre genres de graminées, Cymbopogon, Digitaria, Ehrharta *et* Stipagrostis, *sont cartographiées pour montrer que la spéciation au sein de la phytochorie où un genre a connu une diversification évolutive importante ('sympatrie phytochoriale'), peut être différenciée de la spéciation au sein d'une phytochorie qui ne présente pas cette caractéristique ('allopatrie phytochoriale').*

La vérification de cette hypothèse semble offrir un fructueux champ de recherches pour les systématiciens et améliorera notre connaissance de la flore.

INTRODUCTION

Speciation environments are areas where speciation (micro-evolution) is rapid or has been so in the recent past. It is important to define speciation environments not only for what this can tell us about the factors involved in micro-evolution of particular plant taxa, but also for what we can learn about the evolutionary process by examining the environments in which it is especially active. However, in attempting to define speciation environments for southern Africa, it has become obvious that a number of concepts and assumptions from taxonomy, phytogeography and chorology, biosystematics, ecology and evolutionary theory had to be examined in some detail. A review of the literature pertinent to these problems has been compiled by Robinson & Gibbs Russell (in press). The aim of the present paper is to interpret the distributions of some southern African taxa in the light of current phytogeographical ideas and to examine these taxa in evolutionary terms. We believe that linking the mechanisms of evolution to phytogeography and chorology, as attempted here, will prove extremely fruitful for both fields.

Phytochoria, regions where large numbers of plant species ranges coincide and where there are numbers of endemics, have been put forward for Africa by several authors, especially White (1971, 1976) and Werger (1978), (Fig. 1.) In southern Africa there are six phytochoria, that fall into three major groups: 1, The Sudano-Zambezian Region and the Indian Ocean Coastal Belt Regional mosaics which both extend into southern Africa from the tropics; 2, Capensis and Karoo-Namib Region which are restricted to southern Africa; 3, Afromontane Region and Afroalpine Region that skip from the southern Cape to east Africa at high altitudes. Each of these groups exhibits one or more of the proposed conditions of a speciation environment discussed by Robinson & Gibbs Russell (in press). Although a number of factors promoting speciation may be active in any phytochorion, each phytochorion is remarkable for at least one of the factors that have been suggested as major factors encouraging speciation, depending on its geographical position and overall climatic conditions.

The Sudano-Zambezian Region and the Indian Ocean Coastal Belt regional mosiac are continuations of tropical areas where, because of the high gamma diversity, speciation has been held to be most active. Stebbins (1974) has questioned this, suggesting that the gamma diversity is high because the extinction rate is low in a favourable tropical environment, not that the speciation rate is abnormally high. On the other hand, Simpson (1977) has pointed out that tropical environments would provide no less opportunity for speciation than other environments.

Capensis is well known for its fine-scale spatial heterogeneity. Topographic, edaphic or other environmental heterogeneity is thought to promote fragmentation of gene pools by providing isolated niches, which may be close together. The work of Lewis & Raven (1958) on *Clarkia* in California and Gentry (1981) on *Passiflora* in South America indicates that edaphic factors alone may be enough to promote speciation.

The Karoo-Namib Region is an arid area with a fluctuating environment. According to the 'species

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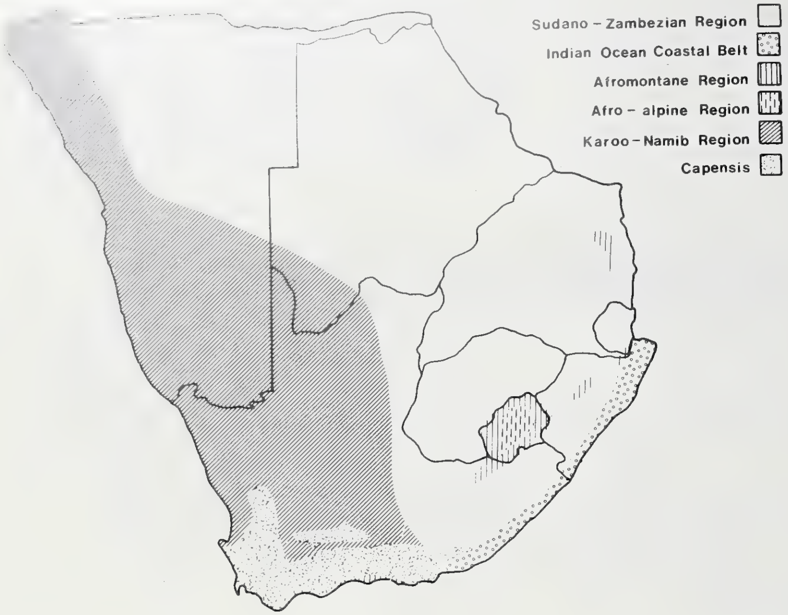

FIG. 1.—Phytochoria of southern Africa, according to Werger (1978).

pump' hypothesis of Valentine (1967), populations may become established during a time of unusually favourable conditions beyond the optimum range of the species. When conditions become severe, these populations will be isolated and therefore could differentiate from the main gene pool of the species. Stebbins (1972, 1974) also takes environmental instability as a key factor encouraging speciation. Arid regions are especially subject to climatic fluctuations, and arid regions for this reason have been strongly suggested by Stebbins (1952), Raven (1964) and Axelrod (1972) as areas that encourage speciation.

The Afromontane and Afroalpine Regions have both fine-scale environmental heterogeneity and local variations in climate brought about by changes in altitude and steep slopes.

In the following discussions, phytochoria are considered to be aggregates of taxa and not geographical areas (Clayton, 1980). We consider that the present phytochoria have existed in some form in the past long enough for the genera which characterize them to have undergone adaptive radiation. However, as climatic conditions have changed, the boundaries of the phytochoria may have shifted according to the tolerance limits of the plants which characterize them. Such a shift is taking place in the eastern Cape Province today as the Karoo-Namib species move eastwards into the Indian Ocean Coastal Belt (Gibbs Russell &

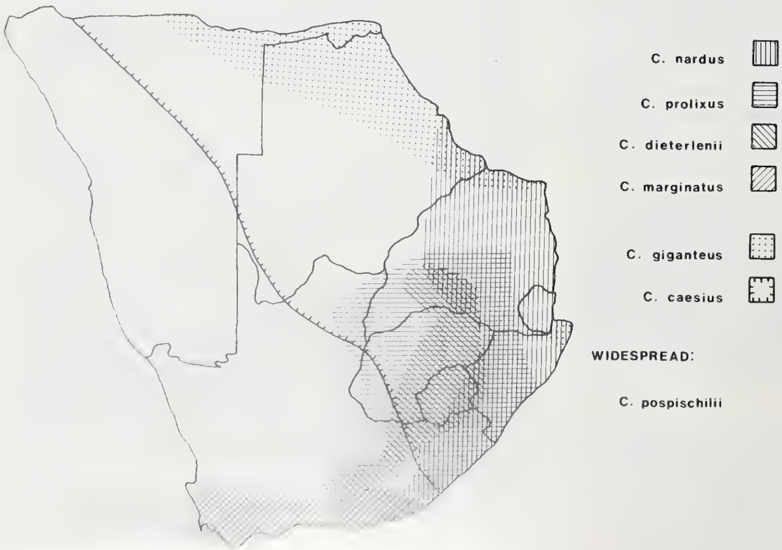

FIG. 2.—Distribution of species of *Cymbopogon* in southern Africa.

Robinson, 1981). The geographical position of a phytochorion is therefore not to be regarded as static, but the environment within it, comprising a set of selection pressures, remains much the same.

The examples of grass genera discussed below show distribution patterns characteristic of the different phytochoria in southern Africa.

DISTRIBUTION PATTERNS

The genus *Cymbopogon* is a tropical genus that shows a decreasing number of species towards the south. Other groups with a similar pattern are *Acacia,* Andropogoneae, Ebenaceae and Combretaceae, all of which are taxa characteristic of the tropical phytochoria in southern Africa, with very few species extending into the winter rainfall region or the arid west. In *Cymbopogon* there are seven species in southern Africa (Fig. 2). Four of these, *C. caesius, C. giganteus, C. pospischilii* and *C. nardus,* extend into southern Africa from a wider distribution in tropical Africa, and the other three occur only in southern Africa, presumably having originated here. Each of the tropical species has a different distribution in southern Africa. *C. caesius* and *C. giganteus* are closely related, and quite distinct from the other species. *C. giganteus* has the smallest intrusion into southern Africa, and is restricted to the tropical parts of the area. *C. caesius* extends further south and west, but is absent from the arid and winter rainfall regions. Neither of these species has given rise to any other extending further south or west than *C. caesius. C. pospischilii* is also quite distinct from the other species, and of all Cymbopogons has the widest distribution in southern Africa, extending into all parts, even the winter rainfall area of the south-western Cape and the arid Karoo and Namib desert.

C. nardus and its closely related species show a different situation. *C. nardus* itself is a tropical species that extends into southern Africa only in the northern and eastern Transvaal, to as far south as Natal, Lesotho and the eastern Cape. It is closely related to three species which are difficult to distinguish from it in some of the regions of sympatry, and which have a wider range in southern Africa than *C. nardus. C. dieterlenii* is restricted to high altitudes in the central Transvaal, the Orange Free State, Natal, Lesotho, and the eastern Cape, with a disjunct spread into the highlands of central South West Africa/Namibia. *C. marginatus* is restricted to the winter rainfall regions of the south-western Cape, and overlaps in distribution with *C. nardus* only in the eastern Cape, which has a variable rainfall regime. *C. prolixus* is imperfectly distinguished from *C. nardus,* differing from it mainly in its smaller size and longer ligule. Although *C. prolixus* does not venture into the winter rainfall regions, it does extend further into the semi-arid west than does *C. nardus.*

When confronted with the varying environments offered by southern Africa, each of the tropical species has behaved differently, and these differences illustrate several of the classic questions of speciation and endemism. Also, the behaviour of each of these species with respect to the phytochorial boundaries gives an indication of the different ways in which plants can respond to major habitat factors that characterize the phytochoria. The alternatives open to any species entering a new area are to spread unchanged (*C. pospischilii*), not to spread at all (*C. giganteus,* and to some extent *C. caesius,* which does not go beyond the borders of the tropical phytochoria) or to associate change and spread (*C. nardus* and its relatives, *C. dieterlenii, C. marginatus* and *C. prolixus*).

The derivitives of *C. nardus* have each originated by a different mode of speciation. *C. marginatus* is clearly allopatric, being totally outside the range of the parental species, and in a different phytochorion as well. *C. dieterlenii* may be an example of parapatric speciation, having arisen in a high altitude habitat surrounded by the range of the parental species. *C. prolixus* may be suggested as a case of stasipatric speciation, because its range overlaps the range of *C. nardus,* except that it extends farther into dry areas. However, until the cytogenetics of these species are worked out this remains speculation. Certainly *C. prolixus* seems more successful than its parent in medium-altitude dry rocky hillslopes, its preferred habitat. It is noteworthy that the only place where all four taxa exist together is the eastern Cape, which is also the only region where all the environmental factors that seem involved in the fragmentation of *C. nardus* occur.

But some basic questions remain unanswered. When spreading into southern Africa, why has *C. nardus* changed and *C. pospischilii* not changed, even though it is the most widespread of the seven species? Why have *C. giganteus* and *C. caesius* not spread beyond the boundaries of their ancestral phytochorion either changed or unchanged? The answer to these questions may lie in the concepts of canalization put forward by Stebbins (1974). Each of the responses to different phytochoria has occurred in a different group of related species in the genus. *C. pospischilii,* which alone has spread unchanged into all the phytochoria, has no near relatives in southern Africa. *C. caesius* and *C. giganteus,* which have not spread beyond their ancestral tropical phytochorion, are closely related to each other but to no other southern African species. *C. nardus* has not itself spread beyond the bounds of the ancestral phytochorion, but its closely related southern African endemic species all stretch into adjacent phytochoria. By Stebbins's proposal, each of the three groups of species has responded in a different way as a result of their inbuilt genetic constraints.

A genus with more species than *Cymbopogon,* also with its distribution centred in the tropical phytochoria is *Digitaria,* which in southern Africa has about 40 species and subspecific taxa (Kok, 1978). (Fig. 3). Three taxa are widespread, *D. sanguinalis,* which is weedy, *D. argyrograpta* and *D. eriantha* subsp. *eriantha,* which are common in a variety of habitats. Thirty of the species are restricted to the tropical phytochoria, some being of more widespread distribution within it than others. Three species, *D. dinteri, D. polyphylla* and *D. seriata,* occur only in the Karoo-Namib and the arid

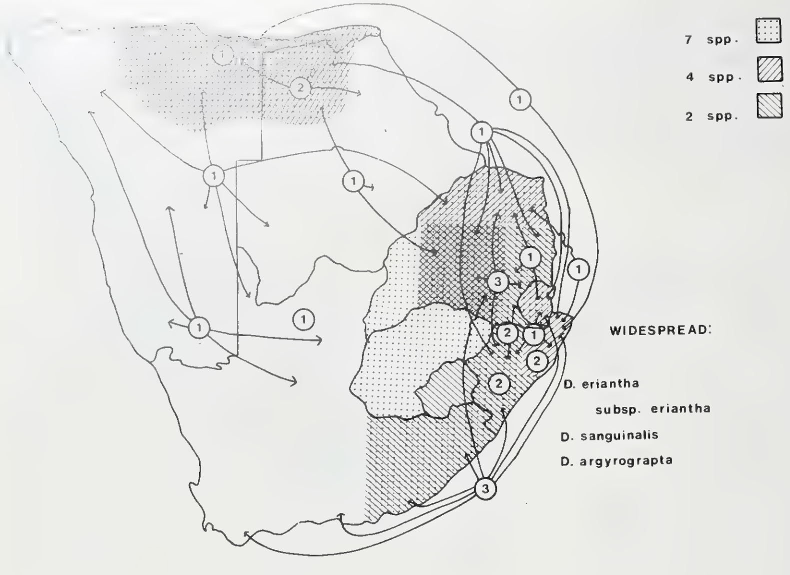

FIG. 3.—Distribution of species of *Digitaria* in southern Africa, based on Kok (1978).

western parts of the tropical phytochoria, and all are very closely related to the widespread *D. eriantha* subsp. *eriantha.* They have apparently been derived from it in a phytochorion outside the ancestral one for the genus. Three species, *D. debilis, D. natalensis* and *D. scalarum,* extend from the tropical phytochoria south-west to Capensis. In contrast to the arid-area species, which are all closely related to a single widespread taxon, each of these is a well-marked species with no very close relatives in southern Africa. Perhaps, as in *Cymbopogon,* it is an indication that canalization may affect the ability of a species to move out of the phytochorion characteristic of its genus.

Ehrharta is a south-western Cape winter rainfall (Capensis) genus of about 30 species and subspecific taxa (Fig. 4). Only two of the species are widespread, five are endemic to the arid north-western Cape and South West Africa/Namibia (Karoo-Namib), one is endemic to the Drakensberg Mountains (Afromontane), and all the rest are restricted to the winter rainfall regions. The Drakensberg endemic, *E. longigluma,* is clearly very closely related to the widespread species, *E. erecta.* Of the five Karoo-Namib species, two, *E. pusilla* and *E. virgata,* are restricted to the southern Namib and Kalahari. Their nearest relative is the widespread *E. calycina.* Two others, *E. barbinodis* and *E. brevifolia* var. *brevifolia,* are centred on Namaqualand, and the nearest relative of each is a winter rainfall species whose range extends just to the southern edge of the dry areas (*E. villosa* and *E. brevifolia* var. *cuspidata* respectively). *E. melicoides,* which occurs from the northern part of the south-western Cape to Namaqualand, is most closely related to *E. erecta,* which is widespread in the winter rainfall and tropical phytochoria, but does not extend into the arid regions.

[illegible] we have a picture of a genus centred on one phytochorion, where it has many species, with a few species that have been able to spread into other phytochoria and have given rise to new species there. The proliferation of species in the south-western Cape has been well documented in a number of genera (Weimarck, 1941; Goldblatt, 1978; Oliver, 1977), and is an example of parapatric speciation in an area remarkable for the variety of habitats available over short distances, in altitude, slope, available rainfall, edaphic factors, etc. The origin of endemic species at the ends of the ranges of the widespread species are examples of allopatric speciation taking place in arid (*E. melicoides*) or mountainous areas *(E. longigluma).*

Another grass genus, *Stipagrostis,* (De Winter, 1965) has its largest number of species in the arid areas of South West Africa/Namibia and the north-western Cape (Karoo-Namib). (Fig. 5.) One species is endemic to the winter rainfall region, (Capensis) and four species are found in the summer rainfall regions (Sudano Zambezian and Indian Ocean Coastal Belt), three of these being endemic to fairly small areas. *S. zeyheri* subsp. *zeyheri,* the south-western Cape taxon, is linked to the main distribution area of the genus through its nearest relative, *S. zeyheri* subsp. *macropus,* whose range is from the northern part of the south-western Cape to Namaqualand. The four taxa from the summer rainfall area fall into two groups. Two are subspecies in a complex that includes the two winter rainfall taxa mentioned above. *S. zeyheri* subsp. *sericans* is restricted to the highveld grasslands of the Sudano Zambezian phytochorion, and *S. zeyheri* subsp. *barbata* has a narrow range extending along the coast from the eastern Cape to Natal, in the Indian Ocean Coastal Belt. The other two, *S. uniplumis* var. *neesii,* widespread in the eastern half of the country, and *S. proxima,* found only in the north-eastern Cape, are closely related to taxa which are widespread in the western half of the country, *S. uniplumis* var. *uniplumis* and *S. namaquensis*

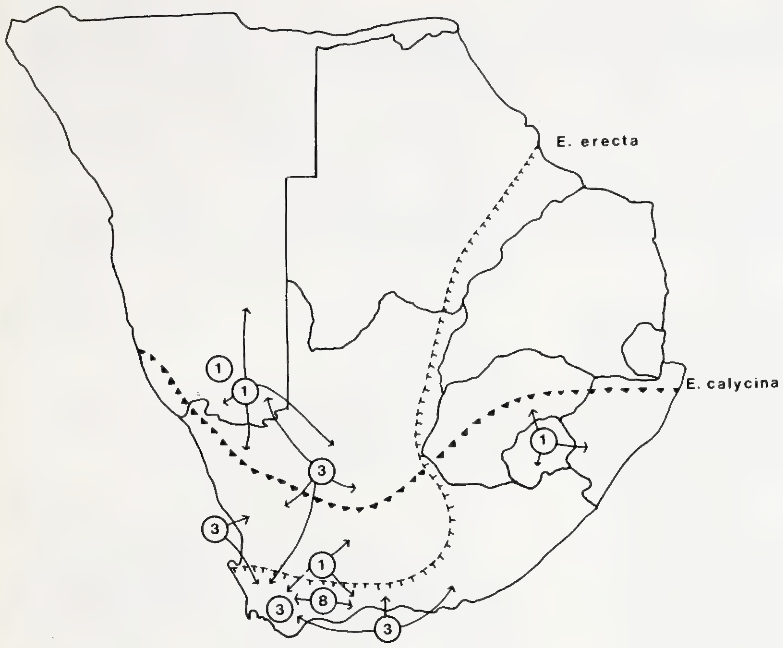

FIG. 4.—Distribution of species of *Ehrharta* in southern Africa.

respectively, and which link them to the main body of distribution of the genus in the Karoo-Namib.

Yet another pattern appears in which there is proliferation of species within a phytochorion, this time in the Karoo-Namib, accompanied by a few species that have spread outside the phytochorion and link endemic species in other phytochoria to the main area occupied by the genus.

CONCLUSION

All these examples show a similar process taking place. In each genus there is a majority of phytochorially sympatric species which have arisen as a result of adaptive radiation in the environment of the phytochorion characteristic of the genus. A few species are able to exist outside the characteristic phytochorion and are widespread. These may

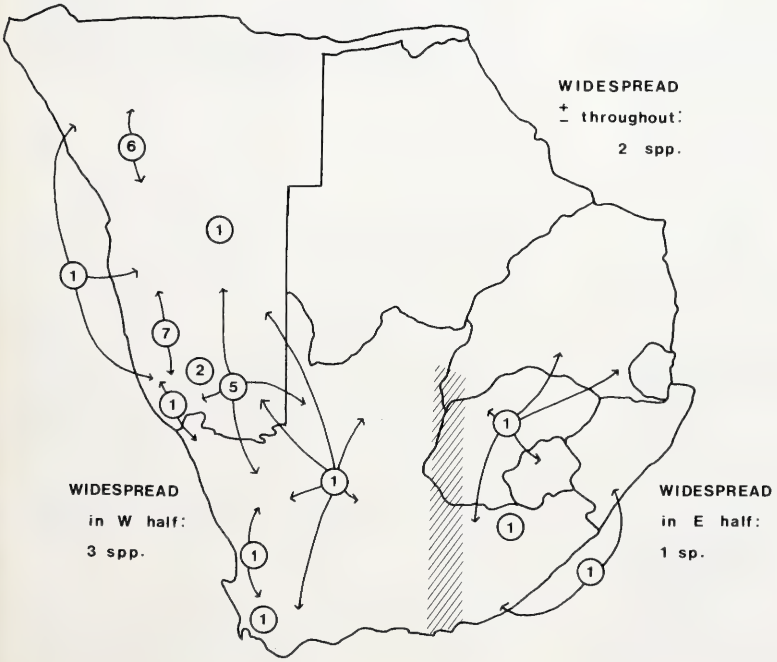

FIG. 5.—Distribution of species of *Stipagrostis* in southern Africa, based on De Winter (1965).

produce secondary species which are phytochorially allopatric to the main area of adaptive radiation of the genus. By the evidence of the examples discussed, these may often be narrow endemics. Finally, allogenous phyletic speciation may occur as some of these taxa extend back into the ancestral phytochorion and hybridize with taxa from which they may be imperfectly separated. It is here that one finds the problems of integradation so difficult to solve by classical taxonomic means.

Phytochorially sympatric speciation may be parapatric or stasipatric. Phytochorially allopatric speciation is allopatric with respect to the species of the original phytochorion, but within the second phytochorion speciation could also be stasipatric or parapatric. It can be followed by allogenic phyletic speciation if these species move back into the ancestral phytochorion. From this, it appears that there is no clear picture of a single speciation environment. Within each phytochorion there have been environments promoting adaptive radiation in genera that are then characteristic of that phytochorion. Outside the ancestral phytochorion there may be new environments promoting speciation in the few species that extend outside the original phytochorion.

It is clear that much basic work is required on aspects such as tests of hypotheses concerning modes of speciation, detailed studies of genetic heterogeneity and its relationship to temporal and spatial environmental heterogeneity, as well as biosystematic studies on major taxa, before fundamental progress can be made in relating chorology to evolution. We believe it is essential that biogeographers and ecologists take more notice of the implications of evolutionary theory for their disciplines.

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Orchids and conservation in tropical Africa and Madagascar

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ABSTRACT

The importance of orchids to the cause of conservation is stressed. Progress in the cataloguing of the orchids of tropical Africa is reviewed and it is concluded that the orchid flora is incompletely known. It is suggested that, to aid the conservationists, authoritative checklists for each country be produced as a prior step to the writing of floristic accounts.

RÉSUMÉ

ORCHIDÉES ET CONSERVATION EN AFRIQUE TROPICALE ET À MADAGASCAR

L'importance des orchidées dans les objectifs de la conservation est soulignée. Les progrès réalisés dans l'inventaire des orchidées d'Afrique tropicale sont passés en revue et il en est conclu que leur connaissance est encore incomplète. Afin d'aider les responsables de la conservation il est suggéré que des catalogues soient préparés pour chaque pays par des spécialistes de la famille avant d'entreprendre leur treitement pour les flores.

Orchids among plants have popular appeal in much the same way as tigers and pandas have in the animal world. In temperate countries such as the U.K., U.S.A. and Japan, conservationists have realised this and have effectively used orchids as an emotive symbol to ensure the protection of threatened environments. The similar use of orchids in tropical countries has been severely hampered by our lack of knowledge of the orchid floras of such regions. Africa is no exception. I would, therefore, like to look in a little more detail at current progress in the cataloguing of the orchids of tropical Africa.

For convenience I will divide tropical Africa into four regions each with a large endemic element and will also consider Madagascar separately.

1. *West and Central Africa.* Summerhayes's (1968a) account of the Orchidaceae in the Flora of West Tropical Africa remains the most useful means of identifying orchids throughout this region. It is still relatively comprehensive for West Africa, although many additional records from former French colonial countries need to be added. For example, Perez-Vera & Cribb (1975) doubled the number of species recorded for the Côte d'Ivoire.

Summerhayes (1968a) is also useful for the Cameroun although far from comprehensive. Sandford has written half of the orchid account for Flore de Cameroun but it has yet to be published. F. W. T. A. Orchidaceae is also useful in Central Africa if supplemented by the Flora of Tropical East Africa Orchidaceae (Summerhayes, 1968b and Cribb, in press), by various papers by Geerinck (1974, 1976, 1977, 1979, 1980) and by Williamson (1977), the last being particularly useful for the orchids of Southern Zaire and Burundi.

2. *Ethiopia.* A checklist of Ethiopian orchids was published by Cufodontis (1972) but it is incomplete. Plans are now well advanced to publish a new Flora of Ethiopia and the orchid account will be jointly written by Copenhagen and Kew. Meanwhile, Summerhayes (1968b) and Cribb (in press) will be useful for all but *Eulophia* species and angraecoid orchids. Similarly, Stewart (1974) contains many species also found in Ethiopia.

3. *Tropical East Africa.* The only relatively comprehensive account of East African orchids remains that of Piers (1968) but, although useful, it is now outdated. Progress with the Flora of Tropical East Africa accounts has been slow but steady since Part 1 (Summerhayes, 1968b) with Part 2 (Cribb, in press) expected later this year and part 3 due to be completed by 1984.

Judging from the results of recent expeditions to Tanzania a great deal still remains to be discovered of its orchid flora which is rich in endemics.

4. *South Central Africa.* Probably the most useful and readily available account for this area is Williamson (1977), which covers the flora of Zambia and to a lesser extent northern Malawi. Checklists exist for Angola (Schelpe, 1976a), Mozambique (Schelpe, 1976b) and Zimbabwe (Grosvenor, 1976).

The epiphytic species of Malawi are dealt with by Morris (1970), but this is now outdated and has been superseded by a more comprehensive account by La Croix *et al.* (1983). Ball (1978) is also useful here and elsewhere in southern Africa.

So far, no start has been made on the Orchidaceae account for Flora Zambesiaca which, presumably, awaits the completion of the FTEA account.

5. *Madagascan area.* The last account of this unique and grossly endangered orchid flora was that of Perrier de la Bathie (1939–41) in Flore de Madagascar. It is now grossly outdated, inaccurate and difficult to use. A new account is desperately needed.

Preparation of an account of the Mascarene species by Bosser is, I believe, well advanced.

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As can be seen, the orchid flora of tropical Africa, despite being much poorer than that of the tropical Americas or Asia, is still incompletely known. This is despite the popularity of orchids in horticulture and their appeal to generations of field naturalists.

If the orchids can be used, as I believe, to promote interest in endangered floras then surely they deserve some priority. Apart from anything else, it makes financial sense to publish orchid accounts as quickly as possible for they easily outsell the others. As a first step then, prior to the writing of floristic accounts, I believe that authoritative checklists for each country should be produced to aid the conservationists who, without these, cannot use these vote winning plants.

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Flora reports

VARIOUS AUTHORS

RAPPORT SUR LA FLORE D'AFRIQUE CENTRALE: 1978–1981

PROGRÈS ACCOMPLIS DANS L'ÉTUDE DE LA FLORE D'AFRIQUE CENTRALE (ZAÏRE - RWANDA - BURUNDI) DE 1978 À 1981

Durant ces quatre années, les fascicules suivants de Spermatophytes ont été publiés: Dipsacaceae (A. Lawalrée & G. Bruynseels, juillet 1979: 6 espèces); Loganiaceae (A. J. M. Leeuwenberg & P. Bamps, juillet 1979: 60 espèces); Myrsinaceae (A. Taton, décembre 1980: 28 espèces et 3 variétés); Pontederiaceae (A. Lawalrée & G. Bruynseels, février 1981: 4 espèces); Potamogetonaceae (S. Lisowski, F. Malaisse, J. J. Symoens & J. Van de Velden, décembre 1978: 5 espèces).

Au total, 103 espèces et 4 variétés ont été décrites.

Pour les Ptéridophytes, aucun fascicule n' a été publié.

PROGRÈS ACCOMPLIS DANS L'EXPLORATION BOTANIQUE DE L'AFRIQUE

L' accroissement des herbiers d' Afrique du Jardin botanique national de Belgique s' est poursuivi de 1978 à 1981 avec les nouvelles collections suivantes (entre parenthèses le nombre de numéros d' herbier):

Ankei: Zaïre (501); *Baecke:* Cameroun (62); *Bamps:* Kenya (456); *Billiet:* Réunion, Maurice (488); *Bouharmont:* Zaïre, Burundi (49); *Breyne:* Zaïre (862); *Bridson:* Rwanda (297); *Bulaimu:* Zaïre (6); *Coppejans:* République sudafricaine et Sud-Ouest africain (1 077); *Darcis:* Zaïre (67); *Dechamps:* Zaïre (85); *Diankenda:* Zaïre (4); *Doutrelepont:* Comores (140); *Dumont:* Zaïre (294); *Evrard:* République sudafricaine et Sud-Ouest africain (479); *Hart:* Zaïre (69); *Kalanda:* Zaïre (20); *Kitembo:* Zaïre (61); *Lambinon:* Rwanda et Burundi (119); *Lebrun:* Zaïre, Burundi, Angola, Zimbabwe, Congo, Cameroun, Ghana, Liberia (260); *Lecomte:* Gabon (12); *Lejoly:* Zaïre (395); *Lewalle:* Maroc (1 665); *Lisowski:* Zaïre, Guinée, Uganda, Tanzanie (2 401); *Lubini:* Zaïre (36); *Mabika:* Zaïre (59); *Malaisse:* Zaïre (1 006); *Malaisse & Gregoire:* Zaïre (6); *Marchal:* Zaïre (56); *Nsimundele:* Zaïre (645); *Nyakabwa:* Zaïre (59); *Pauwels:* Zaïre (412); *Peltier:* Maroc (12); *Poosen:* Zaïre (72); *Rammeloo:* Malawi (500); *Reekmans:* Burundi (1943); *Roche:* Rwanda (111); *Runyinya:* Rwanda (355); *Schaijes:* Zaïre (64); *Sorg:* Rwanda (17); *Tchoume:* Côte d' Ivoire, Sénégal (36); *Tilquin:* Zaïre (19); *Troupin:* Rwanda (370); *Vanden Berghen:* Sénégal (2 055), Canaries (70), Tunisie (137); *Van der Veken:* Niger (61), Burundi (18), Kenya (54); *Verdcourt:* Kenya (80); *Vervaet:* République sudafricaine (14); *Wauters:* Kenya (5)

De plus, le Jardin botanique national de Belgique a reçu du British Museum (Natural History) une série d' environ 6 500 duplicata de la collection LE TESTU (herbiers LE TESTU et TISSERANT) en provenance du Gabon, de la République centrafricaine, de la République du Bénin et du Mozambique.

PROGRÈS ACCOMPLIS DANS LA CARTOGRAPHIE DE L' AFRIQUE

La série 'Distributiones Plantarum Africanarum', éditée par le Jardin botanique national de Belgique, s' est enrichie de 10 fascicules supplémentaires, à savoir:

fasc. 13 (juin 1978): Rubiaceae (E. Robbrecht): 25 cartes; Zingiberaceae (J. M. Lock): 9 cartes.
fasc. 14 (déc. 1978): Ebenaceae (F. White): 55 cartes.
fasc. 15 (juin 1979): Myrsinaceae (A. Taton): 36 cartes.
fasc. 16 (déc. 1979): Rubiaceae (E. Robbrecht): 32 cartes.
fasc. 17 (déc. 1979): Rubiaceae (C. Puff): 26 cartes; Polygalaceae (F. J. Breteler & A. Smissaert-Houwing): 6 cartes; Zingiberaceae (J. M. Lock): 3 cartes; Liliaceae (H. Baijnath): 3 cartes.
fasc. 18 (juin 1980): Orchidaceae (D. Geerinck): 30 cartes.
fasc. 19 (juin 1980): Dichapetalaceae (F.J. Breteler): 32 cartes.
fasc. 20 (juin 1980): Myrsinaceae (A. Taton): 24 cartes; Index des fascicules 1–20.
fasc. 21 (juin 1981): Rubiaceae (C. Puff): 22 cartes; Rubiaceae (E. Robbrecht): 12 cartes; Rubiaceae (E. Robbrecht & C. Puff): 2 cartes; Rubiaceae (D. Bridson): 1 carte; Apocynaceae (F. Kupicha): 3 cartes.
fasc. 22 (déc. 1981): Orchidaceae (H. P. Linder): 25 cartes; Apocynaceae (A. C. Plaizier): 5 cartes; Rubiaceae (E. Robbrecht): 2 cartes.

Diverses autres cartes ont été publiées dans le Bulletin du Jardin botanique national de Belgique et dans le Bulletin de la Société royale de botanique de Belgique par les auteurs suivants:

BAMPS, P. & LEJOLY, J. 1981. Une nouvelle espèce de *Phyllobotryum* (Flacourtiaceae) en Afrique centrale. *Bull. Jard. bot. nat. Belg.* 51: 423–426. 2 cartes représentant 2 espèces au Zaïre.

DENYS, E., 1981. Les *Lasianthus* Jack. (Rubiaceae) du Zaïre, du Rwanda et du Burundi. *Bull. Jard. bot. nat. Belg.* 51: 445–456. 4 cartes représentant 5 espèces au Zaïre.

KUPICHA, F. K., 1981. Studies on African Apocynaceae: two new taxa in *Alafia* Thouars. *Bull. Jard. bot. nat. Belg.* 51:

153–163. 1 carte représentant 2 espèces et 2 sous-espèces en Afrique.

Lejoly, J. & Lisowski, S., 1981. Présence d' *Oxalis barrelieri* au Zaïre. *Bull. Jard. bot. nat. Belg.* 51: 359–365. 1 carte représentant 1 espèce au Zaïre.

Lejoly, J. & Lisowski, S., 1981. Nouvelles données concernant la distribution géographique en Afrique centrale de *Trichocladus ellipticus* Eckl. & Zeyh. subsp. *malosanus* (Bak.) Verdc. (Hamamelidaceae). *Bull. Jard. bot. nat. Belg.* 51: 427–430. 1 carte représentant une espèce au Zaïre.

Rasmussen, F. N. & H., 1979. Notes on the morphology and taxonomy of *Diceratostele gabonensis* (Orchidaceae). *Bull. Jard. bot. nat. Belg.* 49: 139–148. 1 carte représentant 1 espèce en Afrique.

Robbrecht, E., 1978. *Sericanthe,* a new African genus of Rubiaceae (Coffeeae). *Bull. Jard. bot. nat. Belg.* 48: 3–78. 1 carte représentant 1 genre avec ses composantes phytogéographiques en Afrique.

Robbrecht, E., 1979. The African genus *Tricalysia* A. Rich. (Rubiaceae - Coffeeae). 1. A revision of the subgenus *Empogona. Bull. Jard. bot. nat. Belg.* 49: 239–360. 9 cartes représentant 1 sous-genre avec ses 4 groupes et 3 espèces en Afrique.

Robbrecht, E., 1981. Studies in tropical African Rubiaceae 1. *Bull. Jard. bot. nat. Belg.* 51: 165–189. 2 cartes représentant 2 genres en Afrique.

Robbrecht, E., 1981. Studies in tropical African Rubiaceae 2. *Bull. Jard. bot. nat. Belg.* 51: 359–378. 1 carte représentant 1 genre en Afrique.

Robbrecht, E. & Puff, C., 1981. *Mericocalyx* Bamps — synonymous with *Otiophora* Zucc. (Rubiaceae). *Bull. Jard. bot. nat. Belg.* 51: 143–151. 2 cartes représentant 1 espèce avec ses 2 variétés au Burundi.

Symoens, J. J., Van de Velden J. & Büscher, P., 1979. Contribution à l' étude de la taxonomie et de la distribution de *Potamogeton nodosus* Poir. et *P. thunbergii* Cham. & Schlechtend. en Afrique. *Bull. Soc. r. Bot. Belg.* 112: 79–95. 2 cartes représentant 2 espèces en Afrique.

White, F., 1978. The taxonomy, ecology and chorology of African Ebenaceae. I. The Guineo-Congolian species. *Bull. Jard. bot. nat. Belg.* 48: 245–358. 12 Cartes représentant 1 genre avec ses composantes phytogéographiques, 1 section et 3 espèces en Afrique.

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PLANT EXPLORATION IN UGANDA

The Map of Uganda shows its situation and neighbouring territories. It lies in the heart of Africa and is between latitudes 1°30′ south and 4° north; longitudes 29° and 35° east. It is about 1 300 km from the eastern coast. The land mass and lakes have varying altitudes above sea level. In the east, it borders Kenya, in the west Zaire, in the north Sudan and in the south Rwanda and Tanzania.

Uganda is referred to as a crossroads of continental vegetation. There is the Sahara vegetation represented by the north-eastern succulent scrubland. From neighbouring Tanzania in the south, Miyombo savanna-vegetation crosses the country into Sudan. The west African vegetation can be found in the south-west highlands of Uganda and the Semliki Forest in the western rift valley. The Mau Plateau vegetation from western Kenya occupies the eastern grasslands. There are three high mountains namely the Ruwenzoris, Elgon and Mufumbiras. Ericaceous zones occur on these mountains, adding a temperate type of vegetation to the rich Ugandan flora.

Each type of vegetation is very diversified. An example is the lake shore forest which is dominated by *Piptadeniastrum* in the upper storeys, whereas the lower storeys are composed of very many different genera and species. In some swamp forest areas palms like *Raphia* are characteristic of the formation and may be associated with many species of pteridophytes.

Among the many water plants, *Cyperus papyrus* is a common sedge found on rivers and lake edges. Other plants are small and free floating, for example species of *Utricularia*.

Arable lands have a flora of their own. It is a flora which has evolved through ages of land use. *Bidens* [illegible] and many others are noxious

It is this richness and diversity of flora and vegetation that stimulated plant exploration of Uganda. First and foremost were the early continental explorers. Among many others was Emin, who is commemorated in the tree *Maesopsis eminii,* one of the commonest and most useful plants in Uganda. The continental explorers were followed by scientists, whose collections were sent to European herbaria.

In the late 19th century, a scientific department was set up in the country. Among other things, its object was the collection and study of Ugandan plants of economic importance. It began with the founding in 1898 of the Entebbe Botanical Garden and the herbarium now known as the Kawanda Herbarium. The herbarium was later moved to Kawanda Agricultural Research Station. It is housed and shares a room with an insect museum in a complex of administrative buildings. Among the notable collectors in Uganda was Purseglove, who collected many specimens. He was once an agricultural officer in the district of south-western Uganda. The early thirties and late forties were characterized by a spate of plant collecting. However, amongst local scientific workers, political awareness appeared earlier than scientific awareness.

When the expatriate experts left the country, there was nobody to curate the herbarium collections. Sometime before Uganda became independent, the Kawanda Herbarium came to a standstill. Maintenance of the existing specimens fell below normal standards. As a result, some sheets, about 12%, have been destroyed: instead of the original 25 000 specimens there are now 22 000. However, it is gratifying to report that a fresh and dedicated effort has been organized at the Kawanda Agricultural station. The herbarium now has a graduate curator presently training abroad, an assistant curator and assistants. 3 310 specimens were collected and incorporated into the herbarium during the period 1978–1980. This means that before 1978 the number of specimens amounted to 18 690.

In 1900 Entebbe Herbarium proper was established under the management of Forest Department staff. As with its sister herbarium at Kawanda, plant collecting was marked by alternating periods of enthusiasm and disinterest, although plant collecting by the staff was encouraged. After independence, nothing further was added to the number of specimens. In 1979 all the cupboards were looted immediately after the war of liberation. The specimens were displaced and 80% were destroyed. This herbarium is in a hopeless condition. It requires immediate assistance, if the remaining specimens are to be saved. There is a minimum maintenance of specimens, but expert advice is required.

Makerere University Herbarium is housed in one of the rooms in the Faculty of Science. The collections were started by the staff and students of the Botany Department in 1946 and collecting is still being continued. However, in the late sixties the herbarium received a grant and experts from Norway. With this assistance, it was possible to establish the post of curator, assistant curator and two assistants. A plant collection programme was drawn up whereby a number of specimens were acquired. The original number of 6 000 specimens rose to over 25 000. However, the grant and programme expired and the experts left the country in 1972. The economic crisis obtaining then forced the assistants to look for better opportunities in other fields, and the assistant curator was obliged to run the herbarium single-handed. During this trying period, materials like spirit, paper and poison could not be obtained. Herbarium pests have invaded the cupboards and 6% of the sheets have been destroyed. There is a faint hope, however, that a graduate assistant will be appointed and earmarked for the post of curator of the herbarium.

Makerere University herbarium is associated with a small botanic garden. The garden has suffered from lack of funds. Labels are missing; a few ponds containing aquatics are kept mainly for teaching purposes; and the greenhouse and orchid shed are worthless. The greenhouse is a mere frame structure and the orchid shed contains hardly any orchids.

CONCLUSION

In this report I send an SOS to the AETFAT Congress. The three herbaria and the gardens have no expert, adequate and experienced research workers. Left alone, the prospects of progress for these herbaria and gardens are quite remote. It is suggested that the three herbaria be brought together and that an international hand be extended in the form of aid to undertake firstly, rehabilitation, secondly staffing and thirdly extension of research to a time when local staff would be in a position to run the amalgamated herbarium. Much plant exploration remains to be done, especially in the western region, and economic uses of indigenous plants need to be studied.

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FLORA ZAMBESIACA PROGRESS REPORT

Vol. IV of which an advanced copy was presented at the IX Plenary Meeting of AETFAT in Las Palmas was published in early summer 1978. It is the first volume of Flora Zambesiaca not printed in parts and contains the families Rosaceae–Cornaceae (658 pp., 170 line drawings, colour frontispiece).

Vol. VII, Part I is now with the printers and should be on the market in January 1983 at the latest. It covers the following families: Crassulaceae (left out of Vol. IV because of technical difficulties), the Valerianaceae and Dipsacaceae [included in this volume in order to render the planned Vol. VI (Compositae) more compact] and then in systematic sequence the families Campanulaceae–Loganiaceae.

In preparation is the first part of the Compositae. Work on this volume was greatly slowed down by the early retirement of its main author the late Professor Hiram Wild. Every effort will be made to print this important part in the course of 1984. Work on the second part is in progress.

The following major families, which will form Part 2 of Volume VII and Part 1 of Volume VIII, are being studied at present: Apocynaceae, Gentianaceae, Convolvulaceae, Verbenaceae, Bignoniaceae, Boraginaceae and Scrophulariaceae. These families are scheduled for publication in 1984/5.

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PROGRESS REPORT ON THE FLORA OF SOUTHERN AFRICA (F.S.A.)

1. *Published and/or distributed since last meeting*

(a) *Introductory volumes and ancillary publications*

1. Bibliography of South African Botany (up to 1951).
2. The Bryophytes of Southern Africa. An annotated checklist. *Mem. bot. Surv. S. Afr.* 43 (1979).
3. Provisional check-list of the pteridophyta for the Flora of Southern Africa. (Lithographed, 1979).
4. Register of plant taxonomic and related projects in Africa (Microfiche, 1978).
5. Do. (Microfiche, 1980).

(b) *Other volumes*

Cryptogams

Vol. 9: Characeae (1978) 45 spp.

Flowering plants

Vol. 10,1: Loranthaceae, Viscaceae (1979) 54 spp.

Vol. 27,4: Asclepiadaceae: *Brachystelma–Riocreuxia* 130 spp.

Introductory volume: Botanical collectors in Southern Africa by Mary Gunn & L. E. Codd (1981).

Cryptogams

Bryophyta: Sphagnaceae–Grimmiaceae 191 spp.

2. *Being edited*

Flowering plants

Vol. 4,2: Mayacaceae–Juncaceae 80 spp.

Vol. 7,8: Iridaceae: *Syringodea–Romulea* 77 spp.

Vol. 21,1: Tiliaceae 50 spp.

Ancillary: A catalogue of South African green, brown and red marine algae.

3. *In advanced to final stage of preparation*

Cryptogams

Pteridophyta ± 245 spp.

Flowering plants

Vol. 3,1: Cyperaceae: *Mariscus* ± 65 spp.

Vol. 5: Liliaceae: Dracaenoideae &
Asparagoideae ± 47 spp.
Caudibracteateae ± 43 spp.
Ornithogaleae ± 126 spp.

[illegible] inder) ± 700 spp.

[illegible] ± 500 spp.

Vol. 9,2: Proteaceae ± 400 spp.

Vol. 10,2: Polygonaceae, Amaranthaceae ± 100 spp.

Vol. 11,8: Mesembryanthemaceae: *Lampranthus* ± 75 spp.

Vol. 14: Crassulaceae ± 227 spp.

Vol. 16: Papilionoideae: *Eriosema* ± 40 spp.

Vol. 18,3: Burseraceae–Malpighiaceae ± 40 spp.

Vol. 21,1: Malvaceae ± 125 spp.

Vol. 23: Penaeaceae–Thymelaeaceae ± 200 spp.

Vol. 28,4: Lamiaceae ± 250 spp.

Vol. 33: Asteraceae: *Helichrysum* et al. ± 330 spp.

4. *Progressing well*

Vol. 2: Poaceae
Vol. 6: Amaryllidaceae
Vol. 17,1: Geraniaceae
Vol. 18: Rutaceae
Vol. 19,1: Anacardiaceae
Vol. 24,1: Myrtaceae, Onagraceae, Araliaceae
Vol. 25: Ericaceae
Vol. 27,1: Periplocaceae
Vol. 27,2: Asclepiadaceae: *Schizoglossum*
Vol. 27,5: Asclepiadaceae: Stapelieae
Vol. 31: Rubiaceae, Dipsacaceae
Vol. 32: Campanulaceae

5. *New format*

As you may be aware the format of the Flora was modified to speed up production of the work without loss of essential information. Fascicles with a minimum of about 50 species are being published, descriptions have been shortened and the citation of specimens has been simplified.

6. *Invitation to contribute*

Forty-eight taxonomists from outside the Botanical Research Institute are presently co-operating on the F.S.A. Without their work the project could not be completed in the foreseeable future. More help is needed, however, and AETFAT members willing to consider contributing to the project are invited to contact the author.

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THE PRETORIA FLORA

This is a guide to the 1 700 indigenous and naturalized species of ferns and flowering plants of the Pretoria region. It is written, as far as possible, in non-technical language. All species are illustrated by means of line drawings. Comprehensive keys to families and species are based on readily visible characters. A vegetative key to trees is provided but flowering and/or fruiting material is generally required for the identification of other species. Family descriptions are largely diagnostic and mention only characters found locally. Species descriptions are incorporated in the species key with the diagnostic characters printed in italics. Together with notes on ecology and sometimes economics, species descriptions are on average 40 to 50 words long. Recent synonyms and some common names are given. On average six species are dealt with on each text page. Texts are printed on the left hand page and the corresponding illustrations on the page opposite. Introductory chapters deal briefly with ecology and seasonal features of the flora. Publication is projected for 1984.

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PROGRES ACCOMPLIS DANS LA CONNAISSANCE DES FLORES DU CAMEROUN ET DU GABON

FLORE DU CAMEROUN

Au 31 mars 1981, 21 fascicules ont été publiés, comprenant 82 familles dont 26 de Ptéridophytes, soit 405 genres et 1 236 espèces, la flore de ce territoire étant estimée à 230 familles environ, 180 genres et plus de 8 000 espèces.

— Volumes parus depuis le 31 juillet 1977: 20, Chrysobalanaceae, Scytopetalaceae, Rosaceae; 21, Cruciferae, Cochlospermaceae, Dipsacaceae.

— En cours d'impression: 22, Balsaminaceae, Xyridaceae; 23, Loranthaceae; 24, Melastomataceae.

— En préparation: Moraceae, Amaryllidaceae, Helobieae, Annonaceae.

Depuis le fascicule 21, la rédaction continue à être assurée par le Laboratoire de Phanérogamie du M.N.H.N. de Paris, mais l'édition est réalisée par la DGRST du Cameroun sous la direction de B. Satabie et J.- F. Leroy.

Documents phytogéographiques du Cameroun: publiés sous forme de fiches avec cartes au 1:5 000 000 et concernant uniquement les arbres et les arbustes. R. Letouzey et Coll.: n°1, 130 fiches, 1978.– n°2, 118 fiches, 1979.

FLORE DU GABON

24 fascicules ont été publiés comprenant 85 familles dont 23 de Ptéridophytes.

— Volume paru depuis le 31 juillet 1977: 24, Chrysobalanaceae, Scytopetalaceae.

— En cours d'impression: 25, Moraceae.

— En préparation: Dichapetalaceae.

Publications diverses: 44 articles sur la flore africaine sont parus dans *Adansonia,* contenant pour la plupart une étude systématique ou morphologique d'espèces camerouno-gabonaises dans diverses familles.

Pour le Gabon en particulier: publication de la 6e liste des Phanérogames avec 313 espèces et 61 nouvellement citées pour cette région et une étude du couvert végétal en forêt dense humide.

Thèses de doctorat

A. Le Thomas: Interprétation phylogénique des Angiospermes primitives à la lumière des caractères ultrastructuraux du pollen des Annonacées africaines. Université de Montpellier, 1978. Publication en anglais dans Pollen et Spores 22(3–4),1980, 23(1),1981.

J.- F. Villiers: Formations climaciques et relictuelles d'un inselberg inclus dans la forêt camerounaise. Muséum et Université Paris VI, 1981.

A. LE THOMAS*

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REPORT ON THE ADUMBRATIO FLORAE AETHIOPICAE

The series known as *Adumbratio Florae Aethiopicae* was initiated in 1953 by the late Director of the Tropical Herbarium of Florence, Prof. Alberto Chiarugi. Subsequently, direction of the series passed to Prof. R. E. G. Pichi Sermolli, who arranged its scientific programme and prepared an outline for each family.

The Adumbratio was conceived with the intention of producing a critical revision of each species known for the Flora of N.E. Tropical Africa (Ethiopia, Djibouti, Somalia and Socotra). In other words, a true flora was not envisaged and analytical keys and descriptions of species have not been intentionally incorporated.

A standard format has been adopted with the following information provided for each taxon:

Family: literature citation, type genus, taxonomy, nomenclature, general distribution and observations;

Genus and infrageneric taxa: literature citation, type species, synonyms, etymology, taxonomy, distribution and observations;

Species and infraspecific taxa: literature citation, basionym (if any), type, synonyms, taxonomy, nomenclature, etymology, illustrations (an original drawing of a herbarium specimen), localities (within the area concerned and including distribution map), ecology, vernacular names and possible utilization.

The taxonomy is elucidated through a study of herbarium specimens housed in the Tropical Herbarium of Florence (Erbario Tropicale di Firenze – FT) and numerous other herbaria, in particular FI, K, P and the BM, but also ACD, B, BP, BR, C, COI, E, EA, ETH, FR, G, GH, L, LE, N, MEL, MO, N, NA and US, PAL, PRC, S, STR, STU, TO & TOM, UPS, W & WU, WAG and Z.

Revisions of 20 families of Pteridophytes (mainly by R. E. G. Pichi Sermolli) and 16 families of Angiosperms have been published to date. Scientific staff of several Italian botanical institutions (Firenze, Genova and Perugia) and foreign contributors have collaborated in the revison of these families. Other families are presently receiving attention.

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FLORA OF TROPICAL EAST AFRICA

Publicaton of the *Flora of Tropical East Africa* has been interrupted since the East African Community, which provided funds for printing, was dissolved in 1977. The Goodeniaceae (F. G. Davies), Guttiferae (P. Bamps, N. Robson and B. Verdcourt) and Thymelaeaceae (B. Peterson) were published from a residue of former funds in 1978. Thereafter, no practical advance was made, despite extensive consultation, until changes in U.K. Government policy made it possible to offer the publication to private enterprise. In consequence, A. A. Balkema undertook to publish the Flora from the end of 1980 in a format closely matching previous issues.

The Balsaminaceae (C. Grey-Wilson), Cruciferae (B. Jonsell), Gramineae Part 3 (W. D. Clayton and S. A. Renvoize) and Rutaceae (J. O. Kokwaro) are scheduled to appear early in 1982. The following parts are ready for press (Amaranthaceae (C. C. Townsend), Amaryllidaceae (Inger Bjørnstad), Anacardiaceae (J. O. Kokwaro), Cyclocheilaceae (W. Marais), Erythroxylaceae (N. Robson and B. Verdcourt), Ixonanthaceae (B. Verdcourt), Myrothamnaceae (Marie Bywater), Myrsinaceae (P. Halliday), Nesogenaceae (W. Marais), Orchidaceae Part 2 (P. J. Cribb), Palmae (J. Dransfield), Smilacaceae (E. J. Cowley), Zingiberaceae (J. M. Lock) and Zygophyllaceae (M. N. El Hadidi).

With the publication of these parts, altogether about 1 150 printed pages, the Flora should be more than half complete. There is no cause to revise the estimate in Boissiera 24: 607–608 (1976) of a total vascular flora of 10 000–11 000 species and a completion date around the turn of the century. Nevertheless, the relative escalation of printing costs is worrying. It is convenient at this time to list the parts published with their revised prices. They are obtainable from A. A. Balkema, Box 1675, 3000 BR Rotterdam, Netherlands (for U.S.A. and Canada: 99 Main Street, Salem NH 03079); Publications Department, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, England; Government Bookshop, Box 569, London SE1 9NH, England; Text Book Centre Ltd., Kijabe Street, Box 47540, Nairobi, Kenya; Government Publications Agency, Box 1801, Dar es Salaam, Tanzania and Government Printer, Box 33, Entebbe, Uganda.

Parts published to date are as follows:

Foreword and preface	0.50
Glossary	£1.00
Aizoaceae, 1961, 37pp., 11 figs	£1.00
Alangiaceae, 1958, 4pp., 1 fig.	0.50
Alismataceae, 1960, 16pp., 7 figs	£1.00
Annonaceae, 1971, 128pp., 29 figs	£3.20
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Araliaceae, 1968, 23pp., 5 figs	£1.00
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The most notable extensions of East African botanical exploration in the last five years have been in the Selous Game Reserve of SE Tanzania [see Vollesen in Opera Botanica No. 59 (1980)] and in the northern parts of Kenya around Kulal [see Hepper, Jaeger *et al., An annotated check-list of plants of Mt Kulal,* IPAL Tech. Rep. (1982)] and especially towards the Somali border. Collaboration between the University of Dar es Salaam and Kew has led to expeditions by Cribb, Grey-Wilson and Mwasumbi to the Mahenge region (the type locality of many species named from Schlieben collections) and to the Southern Highlands of Tanzania in 1977, and by Hooper, Mwasumbi and Townsend to western Tanzania in 1980. Cribb and Leedal have produced a well-illustrated popular guide to the *Mountain Flowers of Southern Tanzania,* to be published shortly by A. A. Balkema. The University of Uppsala has continued student exchanges with the local universities, with special emphasis on the medicinal plants of Tanzania.

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THE TOGO FLORA PROJECT

The Flora of Togo Project, aiming at the publication of a manual in French on the flowering plant species of Togo, was initiated at the Botanic Museum, Berlin-Dahlem, West Germany, in 1972. It is now nearing completion and the manuscript will go to the press in the near future. The editors are indebted to many persons, both living and deceased, from various countries, who have furthered this Project by collecting plants and by contributing valuable treatments.

The first botanical explorations in Togo were undertaken by army officers, resident collectors and expeditions during the German colonial period from 1884–1914. Engler (1911) presented their results in a rather detailed synthesis. In later years it was mainly French botanists who enlarged our knowledge of the flora of Togo. When the Republic of Togo reached independence in 1966, botanical field work was much intensified. Since 1972 a close cooperation has been established in this regard between the Bénin University in Lomé, the Service de la Protection des Végétaux in Lomé-Cacaveli and the Botanical Museum, Berlin-Dahlem.

The number of plant specimens gathered in Togo during the last ten years exceeds 10 000. To these, 5 000–6 000 brought together in earlier days (Urban, 1917; Hepper & Neate, 1971), may be added. These figures indicate a high level of floristic investigation, which is confirmed by the ratio of specimens to species numbers. The number of species recorded in the Flora of West Tropical Africa (FWTA) in the seven major families (Hepper, 1965, 1972) is approximately three times that which is presently known for Togo (Table 1); by extrapolating the total figure from FWTA (7 037 flowering plant species) one arrives at an estimate of 2 300 species for the flora of Togo (taking into account some distortions, a figure of barely 2 000 species is even more realistic). This means, by definition (Hepper, 1979), that Togo now belongs to the 'well-known' areas of Africa, because 'more than three times as many specimens as species have been collected'.

TABLE 1.—Comparative species numbers for the seven major flowering plant families in Togo (56 600 sq km) and West Africa (4 508 000 sq km)

Family	W. Africa FWTA (1954–72)	Togo Engler (1911)	Togo FWTA	Togo presently known
Leguminosae	728	79	103	297
Gramineae	615	52	110	249
Rubiaceae	559	45	42	129
Orchidaceae	403	8	16	76
Cyperaceae	314	36	64	145
Compositae	293	18	25	95
Euphorbiaceae	275	20	43	89
Total	3 187	258	403	1 080

Recent collections have led to some additions to the 'Flora of West Tropical Africa', in particular and most importantly, to the description of eight new species: *Anadelphia liebigiana* H. Scholz, *Digitaria ursulae* H. Scholz, *Osbeckia togoensis* Leuenberger, *Phyllanthus gagnioevae* Brunel & Roux, *P. magnificens* Brunel & Roux, *P. rouxii* Brunel, *Pseudovigna puerarioides* Ern, and *Schoenoplectus raynalianus* U. Scholz.

The Flora of Togo Manual, which is to be supplemented by a separate, illustrated volume for the Glumiflorae *(Gramineae, Cyperaceae),* will include keys for determination, full citation of known herbarium specimens, and an indication of the distribution within five main phytogeographical subdivisions. Data from the literature are also incorporated completely, even though in some cases it has not been possible to trace and revise the corresponding specimens, many of the older ones being buried in large collections or having been destroyed in World War II. Such unavoidable shortcomings and others that one may detect, will hopefully contribute to stimulate further research.

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H. SCHOLZ*

REPORT ON THE PROGRESS OF CONSPECTUS FLORAE ANGOLENSIS

The political changes that have taken place in recent years both in Portugal and Angola have, to a certain extent, influenced the development of 'Conspectus Florae Angolensis'. In fact, since the last report on the progress of this work was presented viz. A. Fernandes in Boissiera 24: 617–619 (1976), only a single volume has been published, this being the Pteridophyta by E. A. C. L. E. Schelpe (Selaginellaceae and Isoetaceae by E. A. C. L. E. Schelpe & A. C. Jermy, and Marsileaceae by E. Launert). This volume runs to 197 pages with 33 line-drawing plates and covers all 26 families of Pteridophyta that have been found in Angola. It was published in Lisbon on August 25th 1977 by the Junta de Investigações Científicas do Ultramar (Overseas Scientific Research Board) which also funded the publication; the Portuguese version of the English manuscript was prepared by Rosette B. Fernandes and E. J. Mendes.

Meantime, it was decided that the creation of an [illegible] would be desirable, and that all the institutions promoting the project should be represented on this Board, namely the Instituto Botânico da Universidade de Coimbra and the Department of Botany of the British Museum (Natural History), foundation members since the first fascicle of the C.F.A. was published in 1937, the Centro de Botânica da Junta de Investigações do Ultramar which joined them in 1960, and also more recently, in 1980, the Departamento de Ciências Biológicas, of the Centro Nacional de Investigação Científica, Luanda. Those presently representing these institutions as members of the Editorial Board are Rosette B. Fernandes, E. Launert, E. J. Mendes and O. J. A. de Menezes, respectively.

The next fascicle of this work, dealing with the Crassulaceae, by Rosette B. Fernandes, is scheduled for publication at the end of 1981 or the beginning of 1982, and will complete the publication of all the families of the Polypetalae that are known to be represented in Angola. The delay in publishing the study on the Crassulaceae is due to the death at a

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very old age of Raymond-Hamet, who had initially been in charge of studying this family.

The present members of the Editorial Board of the C.F.A. are endeavouring to obtain international assistance from various experts, and the following authors have already promised their co-operation for the preparation of the accounts of the following families: Loganiaceae and Apocynaceae (A. J. M. Leeuwenberg, Wageningen), Ericaceae (R. Ross, London), Lobeliaceae (M. Thulin, Uppsala), Ebenaceae (F. White, Oxford); Portuguese taxonomists have been asked to prepare texts for the following families: Bignoniaceae (E. J. Mendes & Maria Adélia Diniz; LISC); Boraginaceae (E. S. Martins; LISC); Convolvulaceae (Maria Leonor Gonçalves; LISC); Gentianaceae (J. Paiva; COI); Solanaceae (A. E. Gonçalves; LISC) and Verbenaceae (Rosette B. Fernandes; COI). Thus we believe that significant progress in the publication of the C.F.A. will be achieved in the near future.

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REPORT ON THE PROGRESS OF FLORA DE MOÇAMBIQUE

A. Fernandes founded Flora de Moçambique when the Junta de Investigações do Ultramar (Overseas Research Board) recognized the importance of launching the publication of such a flora in the Portuguese language, basically for the use of college teachers and university professors in Mozambique, but also to assist technicians and other persons interested in problems relating to the vegetation of Mozambique, and who might not be familiar with English. Therefore the 17 first fascicles of this work were published in 1969, each covering one Phanerogamic family, and 19 more were published in 1973.

In spite of the political changes that took place in Portugal in 1974, it was possible to resume publication of this flora five years later, with the release of 13 fascicles, 12 of which deal with a single family each of flowering plants, whereas the thirteenth is devoted to all the families of Pteridophyta recorded in Mozambique.

In November 1980 fascicles covering 7 more families were edited. The accounts by J. M. F. Cannon & E. S. Martins of the families Umbelliferae and Araliaceae, and those by E. J. Mendes of Rosaceae (gen. *Rubus* by F. Kupicha), Montiniaceae and Myrothamnaceae have been recently completed and their publication is scheduled for 1981.

Work on this flora continues to progress and is promoted by the Centro de Botânica, of the Junta de Investigações Científicas do Ultramar, which funds publication, the editorial and administrative work being coordinated by E. J. Mendes, with the technical support of the Instituto Botânico of the University of Coimbra, the Departamento de Botânica of the Eduardo Mondlane University, Maputo, and the Instituto de Investigaçâo Agronómica, Maputo. To date, 56 fascicles of this flora have been edited, with 5 more presently in the press and another 5 being actively prepared for publication in 1982, one of these dealing with the sub-family Mimosoideae.

A detailed list of the fascicles of this Flora, published to date, is available on request either to the Serviço de Publicações, Junta de Investigações Científicas do Ultramar, Rua da Junqueira 86, P–1300 Lisboa, or to Publications Sales, British Museum (Natural History), Cromwell Road, London SW7 5BD. The Flora may be ordered by post from either of the above-mentioned agencies.

E. J. MENDES*

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